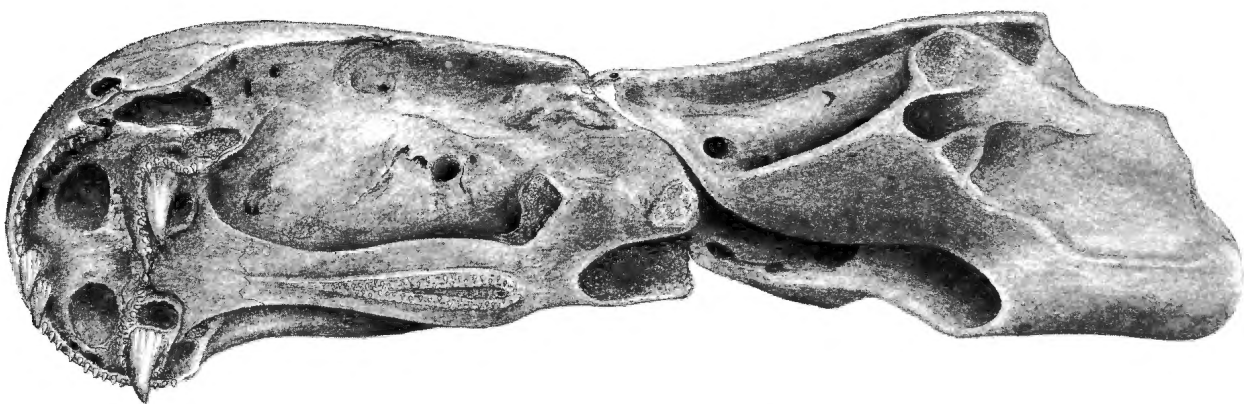


MEMOIRS

OF THE

QUEENSLAND MUSEUM



BRISBANE
1 JUNE 1995

VOLUME 38
PART 1

DICTYOCERATIDA, DENDROCRATIDA AND VERONGIDA FROM THE NEW CALEDONIA LAGOON (PORIFERA : DEMOSPONGIAE)

P.R. BERGQUIST

Bergquist, P.R. 1995 06 01: Dictyoceratida, Dendroceratida and Verongida from the New Caledonia Lagoon (Porifera : Demospongiae). *Memoirs of the Queensland Museum* 38(1): 1-51. Brisbane. ISSN 0079-8835.

Twenty nine species of sponges belonging to the orders Dictyoceratida, Dendroceratida and Verongida are described from the lagoon, and fringing and adjacent reefs of New Caledonia. Of these, eighteen are Dictyoceratida and ten are new species, five are Dendroceratida including two new species, and six are Verongida of which five are new. All represent new records for the region. The fauna cannot be compared with those of Indo-West Pacific, Micronesia and Tropical Australia because of the lack of detailed study and good descriptions in all cases, and because many new genera remain to be described from all regions. Generic and familial diagnoses are included for all species recorded. □ *Dictyoceratida, Dendroceratida, Verongida, New Caledonia, shallow-water sponges, lagoon, new genera, new species.*

Patricia R. Bergquist, Zoology Department, University of Auckland, Private Bag 92019, Auckland, New Zealand; 1 November 1994.

Prior to the work of Hooper & Lévi (1993a, 1993b), only about 170 species of Porifera had been described from the New Caledonian region. For Demospongiae in this region, the major emphasis has been on the deeper water fauna (Lévi & Lévi 1983a, 1983b, 1988, Lévi 1991) and the only record of a sponge belonging to the Dictyoceratida, Dendroceratida or the Verongida, is that of *Ircinia aligera* (Burton) by Lévi and Lévi (1983b). No authors dealing with shallow water faunas have recorded any species from the same three orders. Lévi (1979), in a review of the demosponge fauna of the New Caledonian area, referred to the occurrence of "extensive populations of massive species of *Spongia*, *Dysidea*, *Ircinia*, *Fasciospongia*" and stated that all genera of Dendroceratida were present as was "massive *Psammaplysilla*" (Verongida). These comments are in large measure accurate, but thus far no taxonomic descriptions of this fauna have reached the literature. This deficit for shallow water and reef fauna of the New Caledonian region applied in many sponge groups, but it was most extreme for the three orders considered in this paper.

Based on the excellent sponge collections amassed by ORSTOM over many years, a collaborative project involving New Zealand, French, and Australian sponge systematists was launched. The aim, following a series of workshops and some field work, was to produce a taxonomic inventory of the shallow water fauna and a lay field guide to the major species. It is recognised, however, that many additional spe-

cies remain to be described. For the Dictyoceratida, Dendroceratida and Verongida many species in the ORSTOM collections were represented by single specimens, and in large genera, particularly *Spongia*, *Dysidea* and *Ircinia*, this is inadequate for diagnosis and description of new species.

This work records dominant species which were represented by several specimens, and species where confident identification could be made on the basis of individual specimens. Full descriptions of previously described species are included only where earlier literature is deficient. Colour illustrations envisaged for the field guide will add greatly to the figures included in this manuscript.

METHODS

Methods used to prepare and examine sponges for light microscopy are standard. These, and the characters used in description of sponges belonging to the orders Dictyoceratida, Dendroceratida and Verongida, have been detailed elsewhere (Bergquist 1980). Investigation of terpene composition followed procedures outlined in Bergquist et al. (1990a,b). All skeletal and histological descriptions are based on quoted voucher samples; information on species distribution, ecology, live characteristics are based on personal communication with ORSTOM divers, perusal of their photographic archives, and on discussion with colleagues at the ORSTOM workshops. All colour notations relate to Munsell (1942). Diag-

noses of orders are as given by Bergquist (1980), diagnoses of families and genera, some of which are revised, are given in all cases. Abbreviations used in the text are - AUZ, University of Auckland, Zoology; BMNH, The Natural History Museum, London; ORSTOM, Institut Française de Recherche Scientifique pour le Développement en Co-operation, Centre de Noumea; QM, Queensland Museum, Brisbane.

SYSTEMATICS

Order DICTYOCERATIDA Minchin
Family SPONGIIDAE Gray, 1867

DIAGNOSTIC REMARKS

Dictyoceratida in which the spongin fibres making up the anastomosing skeletal network are homogeneous in cross-section, showing no tendency to fracture around planes of concentric lamination. Fibres contain no pith, but frequently incorporate sandy detritus. There is typically a hierarchy of fibres in terms of orientation and diameter, but primary elements are reduced in some genera. Choanocyte chambers are diplodal, and the matrix is never heavily infiltrated by collagen. The texture of the interior is rough to the touch, reflecting the density of spongin skeleton in relation to soft tissue. The whole body is compressible and resilient except where the surface is heavily sand-encrusted. The skeletal network is never constructed on a precise rectangular pattern. The sponge surface, where not sand-armoured, is always conulose.

Spongia Linne, 1759

Euspongia Bronn, 1859; *Ditela* Schmidt, 1862

TYPE SPECIES

Spongia officinalis Linne, 1759, by subsequent designation (Bowerbank 1862).

DIAGNOSTIC REMARKS

Spongiidae in which the primary fibres are reduced in number and the highly developed secondary network of fine, intertwined fibres makes up the bulk of the skeleton. Primary fibres contain a central axis of foreign material, and are most in evidence near the sponge surface. Secondary fibres contain no foreign material. The texture of

the whole is springy and very compressible, supple and elastic. The surface is never heavily armoured, is covered with low, even, conules, and most frequently is pigmented black, brown, or gray; the interior is white to beige. The form of the sponge is variable, but commonly massive spherical, lamellate, or cupshaped.

TYPE SPECIES

Spongia officinalis Linne, 1759, by subsequent designation (Bowerbank 1862).

Spongia australis sp. nov.
(Fig. 1A-C)

MATERIAL EXAMINED

HOLOTYPE: QMG304682 ORSTOM (R1330) Stn. 198, Chenal des cinq milles, 22°30'04S, 166°45'04E; 20m depth, 11 Feb 1982, Coll. G. Bargibant.

DIAGNOSIS

Steel blue-gray *Spongia* with a sand reinforced dermal membrane and a harsh texture.

DESCRIPTION

A single specimen of this species was available. The sponge body is thick, spreading, 12 by 16cm wide, 5cm deep with irregularly undulating contours and oscular turrets dispersed randomly. The texture is compressible, springy, but firmer than that of commercial quality species of the genus. The oscules are elevated, 3 - 12mm in diameter, pores are small and scattered. The colour is bluish grey in life (P-B ⁵/2), chocolate brown in alcohol (Y-R-Y ⁵/2).

Surface. The surface is microconulose to smooth in patches, slightly abrasive to the touch, as a result of a concentration of sand in the dermal membrane. This forms a layer 50-250µm deep but does not form a compact crust.

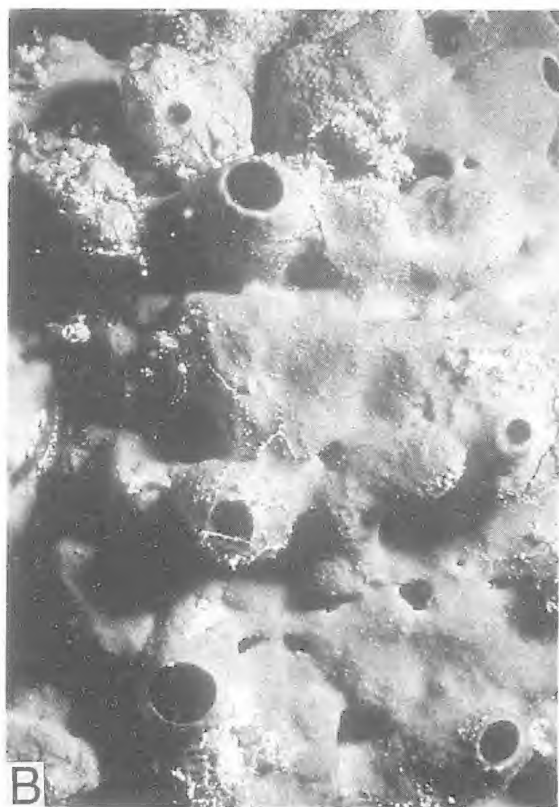
Skeleton. The skeleton is a dense network predominantly of uncored secondary fibres 5-25µm in diameter. Primary fibres are frequent, cored, 40-70µm in diameter, and most evident in the immediate subsurface region. The secondary network is particularly dense around large exhalant canals.

Soft tissue organisation. The soft tissue is evenly and very lightly infiltrated by collagen, with the ectosomal region differentiated only by the presence of large exhalant canals. Choano-

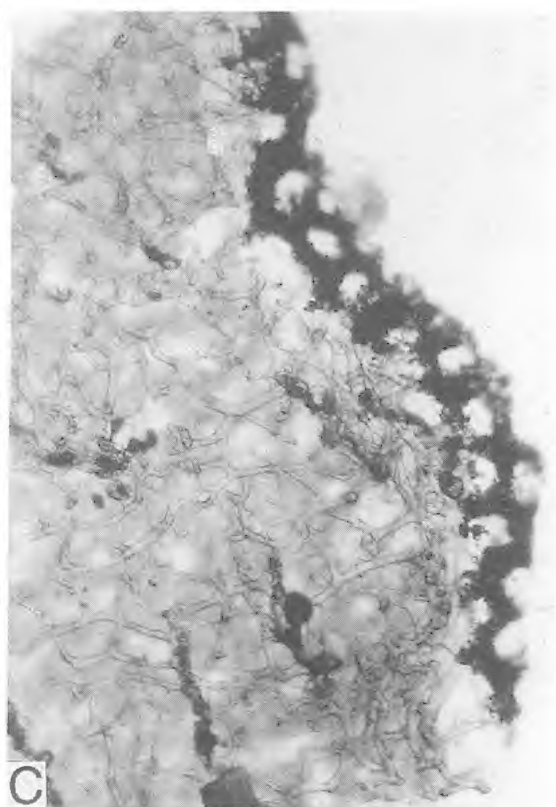
FIG. 1. A-C, *Spongia australis* sp. nov. A, Holotype QMG304682, preserved specimen (x 0.5). B, Holotype QMG304682, in situ (x 0.75). C, Photomicrograph showing primary and secondary skeleton and the dermal sandy layer (x 100).



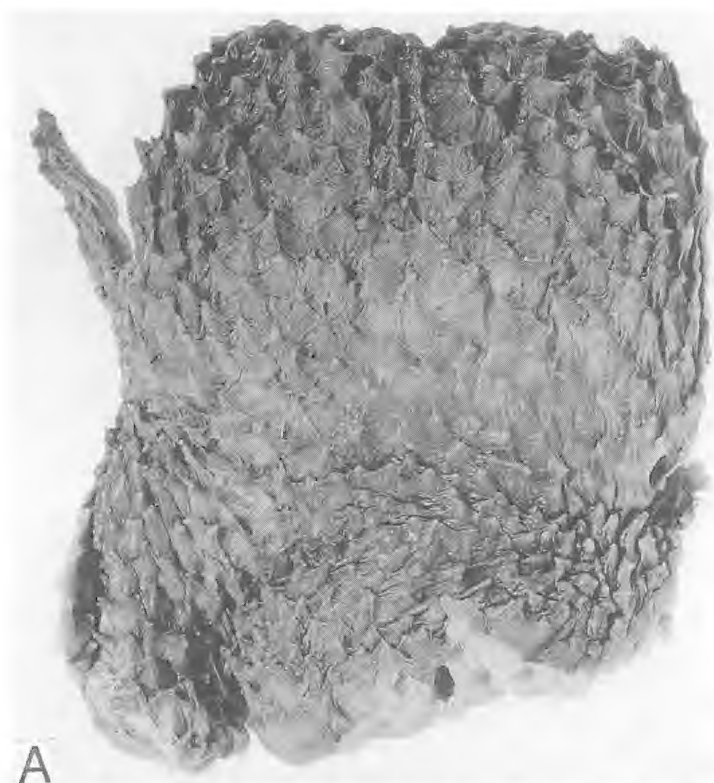
A



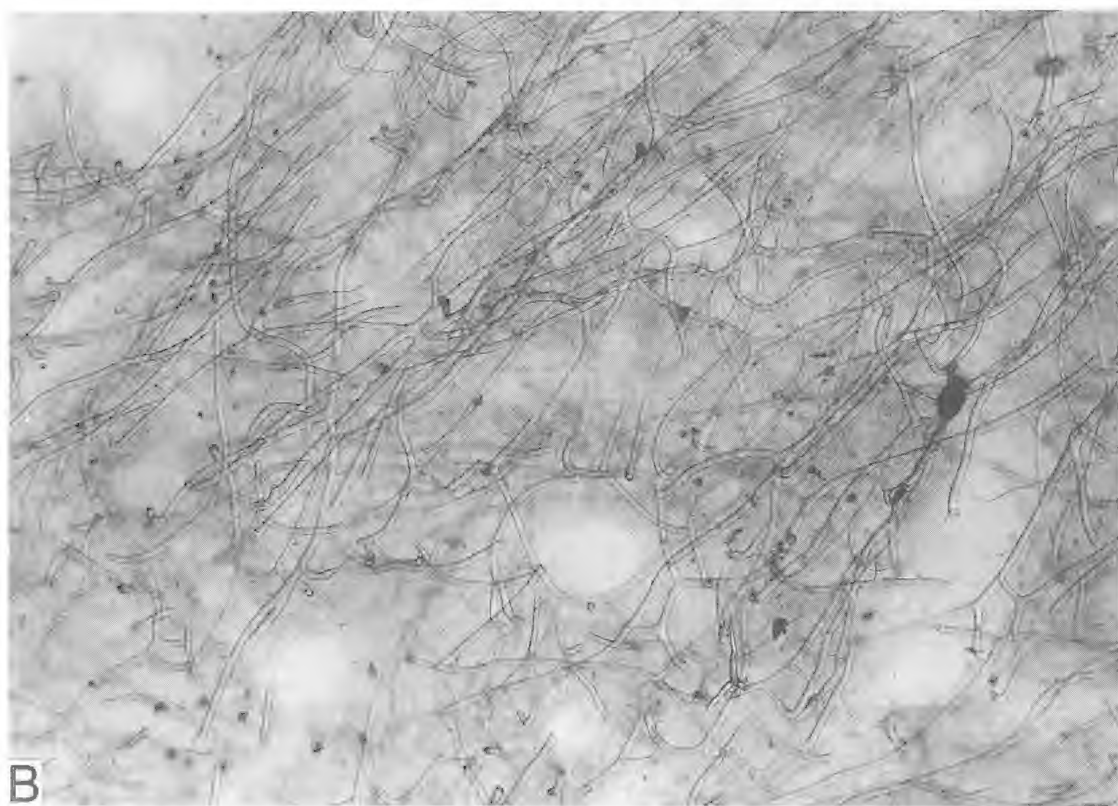
B



C



A



B

cyte chambers are circular, and 15-20µm in diameter.

REMARKS

It is difficult to establish a new species within the genus *Spongia* in which there are many names supported by descriptions which will not permit comparison with newly collected specimens. Most descriptions which deal with species from the southern oceans give no information on colour, surface, texture, habitat, or histology. Since the skeletal characteristics in *Spongia* are relatively invariant, one is left only with gross morphology and geographic distribution on which to base any assignment to an older name. Type material, where extant, is rarely more than a dry skeleton. *Spongia australis* can be distinguished from all other well described species by the steel blue gray colour, the presence of a sand reinforced dermal membrane and by the rather harsh texture.

ETYMOLOGY

The species name refers to the southern ocean distribution of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Coscinoderma Carter, 1883

TYPE SPECIES

Spongia pesleonis Lamark, 1814, redescribed as *Coscinoderma pesleonis* by Topsent (1930).

DIAGNOSTIC REMARKS

Spongiidae in which the primary fibres are cored and the secondary elements are clear, extremely fine, numerous, and intertwined. Carter's analogy with 'whorls of wool' was apt. The surface of the sponge is invested with a sand armour, but the texture remains soft, spongy, and extremely compressible. The sponge body is flabellate, pyriform, massive, or pedunculate, with apical or marginal oscules.

Coscinoderma mathewsi (Lendenfeld) 1886
(Fig. 2A, B)

Euspongia mathewsi Lendenfeld, 1886; 520, pl. 36, fig. 6.

Coscinoderma mathewsi Lendenfeld, 1889; 334, pl. 12, fig. 7; pl. 20, figs. 9, 10.

Hippospongia communis subspecies *ammata*, de Laubenfels, 1954; 9, pl. II, fig. 6.

MATERIAL EXAMINED

HOLOTYPE: BMNH. 86.8.27.301. Dry specimen, Coll. Ponape.

OTHER MATERIAL: MBI P05-80. Coll. Palau, ORSTOM (R664) Stn. 233, Passe de Yandé, 20°05'00S, 161°26'70E, 32m depth, 1 Sept 1978. Coll. P. Laboute.

DESCRIPTION

A single specimen of this species is represented in the ORSTOM collections. It is a massive, hemispherical sponge, 20cm high, 32cm wide with oscules located laterally and apically along low lamellate extensions of the general surface. The texture is extremely soft and compressible, indicative of spongin fibre of the highest quality. Oscules are flush with the surface, 2-6mm in diameter with smooth dermal membrane surrounding and with a slightly elevated elastic lip. Colour in life grayish black, externally, pale yellow/brown internally ($rY^1/6$), in spirit the same. The habitat was coral rubble on the sandy lagoon bottom.

Surface. The surface is strongly conulose with adjacent elements linked by surface tracts to form an intricate regular reticulum. Individual conules are 1-3mm high with rounded tips. The dermal membrane is tightly adherent to the underlying tissue despite the presence of an organised sand cortex 250-350µm deep.

Skeleton. The skeleton is a network of slightly trellised, thin primary fibres which incorporate coring material, and secondary fibres which are thin, vermiform and intertwining. The latter make up the bulk of the skeleton. Primary fibres are 40-100µm in diameter, secondaries 3-12µm in diameter.

Soft tissue organisation. An ectosomal region, 250-350µm deep, is differentiated; it is marked by collagen tracts running parallel to the surface. These provide support and cohesion to the sand cortex. Deep to this region the choanosome has light, uniform collagen deposition and spherical choanocyte chambers 15-30µm in diameter.

REMARKS

Lendenfeld (1885) established this species for a dry sponge from Ponape which he considered

FIG. 2. A,B, *Coscinoderma mathewsi* (Lendenfeld, 1886). A, preserved specimen (x 0.5). B, photomicrograph showing the thin fibres of the secondary skeleton (x 100).

conspecific with *Coscinoderma lanuginosum* Carter. The original description of *C. mathewsi* (as *Euspongia*) is an amalgamation of Carter's description of *lanuginosum* and description of skeletal organisation and dimensions based on the dry specimen of *C. mathewsi*. By 1889 Lendenfeld had revised his earlier view and recognised the genus *Coscinoderma* within which both *lanuginosum* and *mathewsi* were viewed as valid species. He did not add anything to the description of *C. mathewsi* but figured the holotype. This specimen, on re-examination is massive, cake shaped with prominent oscules scattered on the upper, slightly concave surface.

Examination of the of the holotype skeleton confirms the identity of the New Caledonian specimen with *C. mathewsi*. The only other published record of the sponge is by de Laubenfels (1954) as *Hippospongia communis* sub species *ammata* from Kuop Atoll, Ponape and Truk. The habitat he recorded "on the lagoon bottom on dead coral" is identical to the habitat of the New Caledonian specimen. De Laubenfels' description includes an excellent figure (Pl.II, fig.6) of the very distinctive surface of *C. mathewsi*. Bergquist (1980), having examined only the dry holotype, without access to sections, referred *C. mathewsi* to *Spongia*. That decision is revised here.

Other identifications of this sponge have been made by the present author from collections made in Palau by the Marine Biotechnology Institute from Shizuoka, Japan, and from personal collections in Fiji.

DISTRIBUTION

Caroline Islands, Ponape, Kuop, Truk, Palau, Fiji, New Caledonia,

Leiosella Lendenfeld, 1889

TYPE SPECIES

Leiosella elegans Lendenfeld, 1889, by subsequent designation of de Laubenfels (1936).

DIAGNOSTIC REMARKS

Cup shaped, lobed, flabellate or ramose Spongiidae with a skeletal network in which the secondary elements become very dense. The primary fibres are lightly cored and can become fasciculate either where they condense out of the dense secondary network or just below the sur-

face. Some spicule debris can occur in secondary fibres. At the surface there is a thin sand armour, the texture is always firm.

Leiosella ramosa sp. nov. (Fig. 3A, B)

MATERIAL EXAMINED

HOLOTYPE: QMG304683 ORSTOM (R1312) Stn. 323, Récif des Français, 19°11'30S, 163°05'13E, 10-60m depth, 23 Aug 1981, Coll. P. Laboute.

DIAGNOSIS

Leiosella having a ramose form, prominent surficial sand crust and a skeletal network predominantly of secondary uncured fibres.

DESCRIPTION

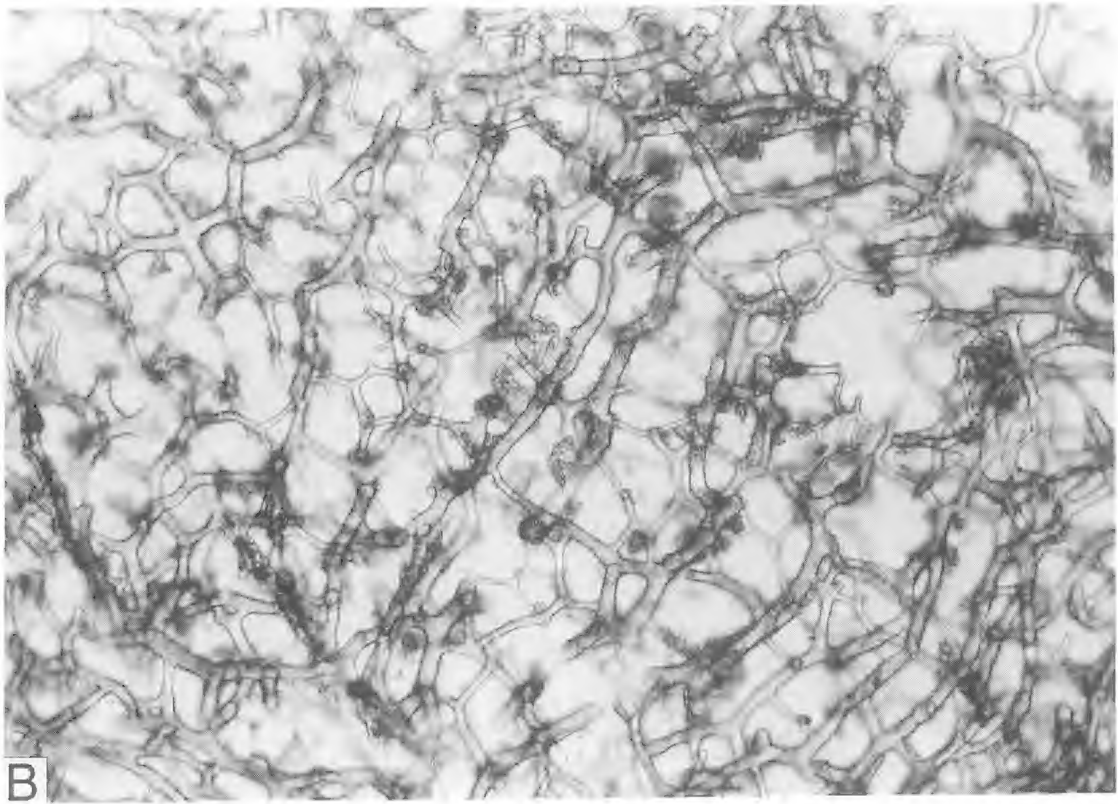
A single specimen was available. It is a ramose sponge branching from a single base of attachment 4cm wide, to a height of 35cm. Stalk and individual branches are elliptical in cross section. The surface is channeled by exhalant canals converging toward the oscules, which are 2-3mm in diameter and located mainly on the sides of branches rather than on the flattened face, and lying flush with the surface. There are areas of the surface in which a white sand crust is evident but this has largely been abraded. Colour in life beige (rY⁶/4), in spirit brown throughout (yY-R⁵/6). The texture is harsh, just compressible.

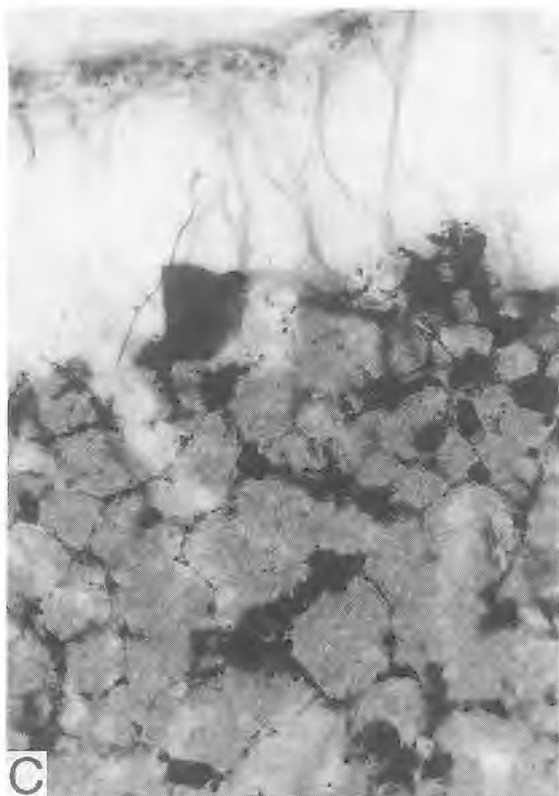
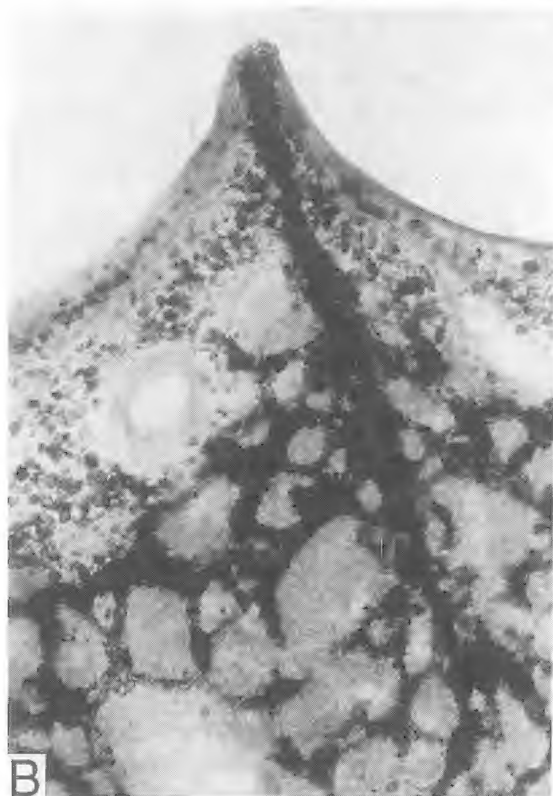
Surface. In life the surface is smooth, dominated by a very finely reticulated sandy crust, which is developed only in the plane of the surface.

Skeleton. The skeleton is a network predominantly of uncured secondary fibres, 10-40mm in diameter, in a very tight anastomosing pattern. Primary fibres are simple and cored, of uniform diameter, 50-70mm, in the deeper parts of the sponge, but becoming fasciculate where they converge toward the surface. The secondary network is compressed and compacted in the 500µm below the surface.

Soft tissue organisation. The density of the fibre network and the condition of the specimen make observation difficult. Collagen deposition is uniform and light, choanocyte chambers are spherical 15-20µm in diameter.

FIG. 3. A-B, *Leiosella ramosa* sp. nov. Holotype QMG304683, preserved specimen (x 0.25). B, Photomicrograph showing primary and secondary fibre skeleton (x 100).





REMARKS

Characteristics of the surface with its prominent sand crust and the organisation of the skeleton place this species within the genus *Leiosella*. Within the genus the ramose form is unique.

ETYMOLOGY.

The species name reflects the ramose form of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Phyllospongia Ehlers, 1870

Mauricea Carter, 1877.

TYPE SPECIES

Spongia papyracea Esper, 1806, by subsequent designation Burton (1934); Cotype BMNH1931.4.1.1a.

DIAGNOSTIC REMARKS

Lamellate, vasiform, digitate or foliose sponges usually of very thin-walled construction, up to 4.0mm thick except in digitate forms which can be up to 1cm in section. Surface is smooth macroscopically, but irregularly corrugated and regularly conulose microscopically. Oscules are small, flush with the surface, or elevated on low mounds emphasised by sand and collagen deposition around each rim. The skeleton is a rectangular reticulation constituted of primary elements disposed at right angles to the surface and secondary connecting elements aligned parallel to the surface. Primary elements may contain coring material, but this is contained well within the investing spongin and never causes the fibre to become irregular in outline. Secondary elements are never cored and are variable in quantity; their relative dominance is proportional to the thickness of the body construction. The pattern of the primary and secondary skeleton is extremely regular and rectangular in very thin species; in those with slightly thicker habit it becomes less regular as the secondary network expands between the primary columns. Tertiary fibrous elements are also present. They are sometimes dispersed, but predominantly are disposed as an axial skeleton. These vermiform elements are invariably present in basal and stalk regions. In forms with digitate

morphology they form marked axial fascicles disposed at right angles to the primary fibres and extending throughout all but the most marginal regions of the body. An organised sand cortex is usually present on one or both surfaces, but it never becomes a pronounced crust as in related genera *Carteriospongia* and *Strepsichordaia*.

Phyllospongia papyracea (Esper) 1806

Spongia papyracea Esper: 1806, 38; *Phyllospongia papyracea* Ehlers, 1870: 22; Bergquist et al., 1988: 304

MATERIAL EXAMINED

COTYPE: BMNH 31.4.1.1a.
ORSTOM (R 1529) Stn. 480, Reef Doiman, 20°35'02S, 165°08' E, 52m depth, 28 Mar 1991. Coll. G. Bargibant.

REMARKS

This species is well known and widespread. It has been described and figured by Bergquist et al. (1988).

DISTRIBUTION

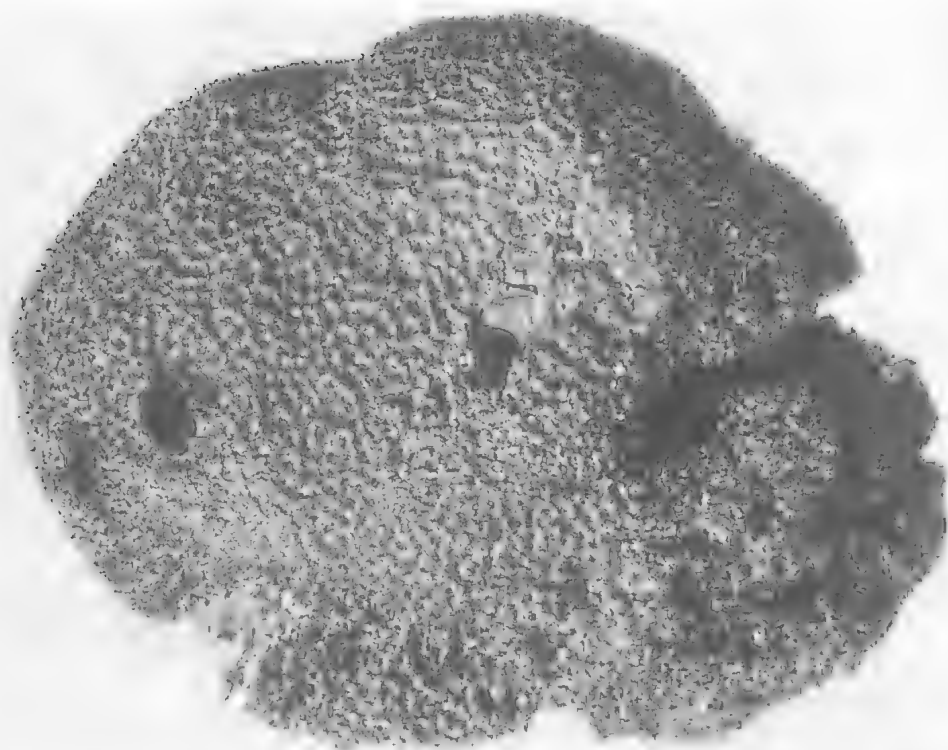
Widespread Indo-Pacific, Northern Great Barrier Reef, Northern Reefs New Caledonia.

Family THORECTIDAE Bergquist, 1978

DIAGNOSTIC REMARKS

Dictyoceratida in which the spongin fibres making up the anastomosing skeleton are laminated in cross-section, with clear zones of disjunction between successive layers. The central region of each fibre is a more diffuse pith; it is not sharply disjunct from the investing more dense layer, as is the pith in the Verongida, but merges into the outer layer. A pith is always evident in the primary fibres and may or may not extend into the secondary elements of the skeleton. The fibre-skeleton is often extremely regular, with almost perfectly rectangular meshes. Some fibres can become extremely stout. Primary fibres can be greatly reduced in number and are lacking in one genus. Choanocyte chambers are spherical and diploidal. The matrix is more collagenous than in the Spongiidae, and macroscopically appears slightly fleshy; its cellular composition can be complex, and some secretory cell types, the

FIG. 4. A-C, *Hyrtios reticulata* (Thiele). A. Preserved specimen (x 0.5). B. Photomicrograph showing coalescence of secondary fibres to produce a short primary tract below a conule (x 80). C. Photomicrograph showing the subdermal lacunae and the clear ectosomal choanosomal boundary (x 80).



A



B

spherulous cells, resemble those of the Verongida. The surface is often armoured in complex fashion, and is frequently thrown into ridges and hollows. Where unarmoured the surface is conulose, and may resemble closely that seen in Spongiidae. The sponge body is often tubular, organised around a series of long, cylindrical canals, and stalked. Yellowish or brick-red internal pigmentation with dark exterior is common. This diagnosis formally differentiates the families Thorectidae and Irciniidae, recognising consistent features of skeletal composition and terpene chemistry within the two groups. The referral of Thorectidae to Irciniidae by Hooper and Wiedenmayer (1994) is not upheld.

Hyrtios Duchassaing & Michelotti, 1864

Oligoceras Schulze, 1879; *Dysideopsis* Lendenfeld, 1888; *Heteronema* Keller, 1889; *Therectopsamma* Burton, 1934; *Inodes* de Laubenfels, 1957.

TYPE SPECIES

Hyrtios proteus Duchassaing & Michelotti, 1864, by subsequent designation of de Laubenfels (1936); re-described by van Soest (1978).

DIAGNOSTIC REMARKS

Thorectidae in which both primary and secondary fibres are fully charged with detritus to an extent which, in some species, can almost obscure the stratified nature of the spongin. The surface of the sponge always retains a distinctly conulose appearance, despite the presence in some species of extraneous detritus throughout the matrix. Primary fibres terminate in the conules, and as a consequence of the sandy inclusions these can appear whitish against the dark sponge surface. The primary skeleton can show some fasciculation near the surface. The texture of the sponge ranges from compressible to quite firm, even brittle, reflecting the degree of development of the skeleton, which in some species can be irregular and reduced, and the extent to which matrix debris is accumulated.

Hyrtios reticulata (Thiele) (Fig. 4A-C)

Dysideopsis reticulata Thiele, 1899: 28, pl.3, Fig. 7.
Hyrtios elegans (pars) Bergquist, 1980: 462.

MATERIAL EXAMINED

HOLOTYPE: BMNH. 08.9.24.213 (ex Berlin).
ADDITIONAL MATERIAL: ORSTOM (R167, R601) Stn.117, Baie de Brony, 22°21'23S, 166°49'30E, 35-40m depth, 30 Jun 1976. (R167), 15 Dec 1977 (R601). Coll. P. Laboute. QMG 304684, ORSTOM (R1315) Stn.323, Récif de Français 19°11'30S, 163°05'13E, 45m depth, 23 Aug 1981. Coll. P. Laboute.

DESCRIPTION

The type description of this species is very brief but with the photograph given by Thiele (1899), and reference to the type specimen, it is possible to assign the New Caledonian specimens to *H. reticulata* with certainty.

The sponge is repent, with cylindrical branches extending upright from the more flattened base. The largest specimen (R.1315) is 40cm long, 15cm wide with individual branches up to 12cm high and 1.5cm in diameter. The sponge is loosely adherent to coral rubble attached at points, but clear of the substrate over most of the basal area. Oscules are 2-5mm in diameter, flush with the surface and scattered over both base and erect branches. A circular area of clear dermal membrane surrounds each oscule. The texture is firm, just compressible. Colour in life gray (yY-R⁵/2) to yellow brown (yY-R⁵/6), in spirit the same. Internal pigmentation is the same.

Surface. The dominant features of the surface are the tracery of radiating ridges extending between conules and the regular distribution of conules themselves. These are sharply pointed and simple rather than multi-tuberculate. They extend 0.3-1.0mm above the sponge surface and give an overall speckled white appearance as a result of exposed fibre coring material.

Skeleton. The skeleton is a compact regular polygonal network of cored fibres, 10-50µm in diameter in which no clear primary fibres are developed except where sectors of the secondary network condense to form a short tract which supports each surface conule. The dermal layer is clear of debris, but a fine layer of debris is organised in the immediate subdermal region. Rare short sections of fibre lack coring material. Clear spongin is always found external to the detrital core of each fibre, and the fibre stratification characteristic of the family Thorectidae is evident. In some other species of *Hyrtios*, fibres are heavily loaded with detritus and structure is dif-

FIG. 5. A,B. *Hyrtios erecta* (Keller). A, apical view of preserved specimen (x 1.0). B, Photomicrograph to show primary and secondary fibres (x 80).

ficult to discern. Detritus extraneous to fibres is absent except in the immediate subdermal region.

Soft tissue organisation. An ectosomal region is clearly set off from the choanosomal region. It is up to 1500µm deep and constituted by the subdermal sandy layer which is supported by a light deposition of collagen. Deep to this is a well developed system of subdermal canals interrupted by thin collagen reinforced tissue tracts. Between conules the skeletal network ends abruptly deep to the canal layer, while below each conule the skeletal reticulum extends to the surface. Choanocyte chambers are spherical, 20-35µm in diameter.

REMARKS

The genus *Dysideopsis* was relegated in synonymy to *Hyrtios* by Bergquist (1980). An attempt was made at that time to assign the species described in *Dysideopsis* to *Hyrtios*, to other genera, or to pronounce them as unrecognisable. *D. reticulata* Thiele was deemed to be identical to *Dysideopsis elegans* Lendenfeld, type species of *Dysideopsis*. Type material of these species, and of the closely related species *Coscinoderma alta*, Polajaeff has been re-examined in the course of this work. As a result, and with the addition of further specimens, it is now proposed to treat all three as distinct species of *Hyrtios*.

Hyrtios is a widespread genus in the Indo Pacific, reaching from the Red Sea (*H. erecta*) to Palau (*H. erecta*), extending into southern oceans on the West Coast of Australia (*H. elegans*) and in Tristan de Cuhna (*H. altus*), represented in the Tropical Central Pacific (Celebes and New Caledonia,) by *H. reticulata*. *Hyrtios erecta* grows to large size, has thick branches (up to 2.5cm diameter), a prominent tracery of dermal tracts and stout, irregular debris packed fibres. It is usually digitate but can be massive and has firm, non-compressible texture. *H. altus* is digitate, has very fine branches 0.8cm in diameter, compressible texture, a strongly conulose surface and fine regular debris packed fibres in which there is no distinction between primary and secondary elements.

H. elegans is very similar to *H. altus* but has short, thick primary fibre tracts identifiable beneath each conule. It is possible that these species are the same, however given the distribution, Port Denison, West Australia for *elegans* and Tristan de Cuhna at 220m depth for *altus*, and the lack of fresh material of either species, the distinction is maintained.

H. reticulata is a clearly distinct species, ramose to digitate with somewhat flattened branches arising from a repent base, harsh in texture like *H. erecta*, having a regular polygonal network of fibres of very uniform dimension which cannot be distinguished as primary or secondary.

From the published descriptions, *Dysidea fusca* Ridley from Torres Strait could be confused with *H. reticulata*. Examination of the type specimen (BMNH 82.2.23.203) confirms that it is a *Dysidea*.

DISTRIBUTION

Celebes, New Caledonia.

Hyrtios erecta (Keller)

(Fig. 5A, B)

Heteronema erecta Keller, 1889: 339; Bergquist, 1965: 129, fig. 2.

Thorectopsamma mela de Laubenfels, 1954: 29, fig. 15, p.8, fig. 6.

Hyrtios erecta Bergquist, 1980: 462, fig. 7c.

MATERIAL EXAMINED

ORSTOM (R1258) Stn. 276, Lagon est, 20°39'00S, 166°26'30E, 20-30m depth, 21 May 1980. Coll. P. Laboute.

REMARKS

The species is common across the Indo Pacific and is well figured and described by de Laubenfels (1954) and Bergquist (1965).

DISTRIBUTION

Indo Pacific (Red Sea to Palau), Great Barrier Reef, Papua New Guinea, New Caledonia.

Petrosaspongia gen. nov.

TYPE SPECIES

Petrosaspongia nigra sp. nov.

DIAGNOSIS

Thorectidae in which cored primary fibres are greatly reduced as a skeletal element, particularly in the choanosomal region. They are most evident in the ectosomal region and form by condensation of many secondary fibres. Coring material is regular and occupies approximately half of the fibre diameter. Secondary fibres form a very dense irregular network and are uncored. The surface is finely and regularly conulose, and encrusted by a fine, evenly dispersed sand layer. The external pigmentation is jet black, the interior is beige to pale

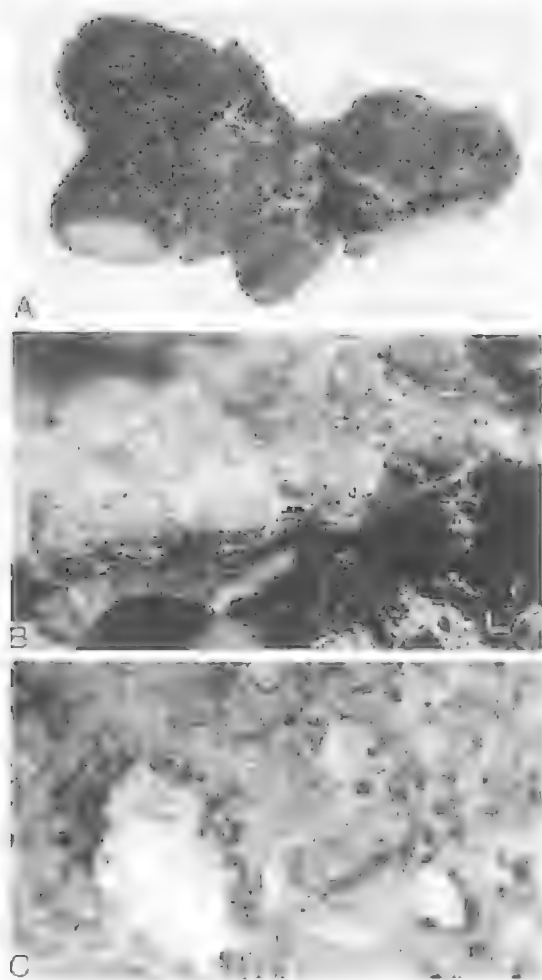


FIG. 6. A-C, *Petrosaspongia nigra* sp. nov. A, Holotype QMG304685, preserved specimen (x 0.25). B, Holotype QMG304685, in situ (x 0.5). C, Photomicrograph showing the dense secondary fibre skeleton and interstitial debris (x 50).

yellow. As a result of the density of the secondary network and the incorporation of moderate amounts of interstitial debris throughout the sponge, the texture is extremely hard and incompressible.

REMARKS

Within the Thorectidae as presently construed, *Petrosaspongia* is closest to *Hyrtios* from which it differs in density of the irregular skeletal reticulum, having uncored secondary fibres which form a very dense network, in the absence of coring

material in the secondary fibres, and in having distinct, but reduced, primary cored fibres. This relationship to *Hyrtios* extends to the secondary metabolite content. Both contain sesterterpenes of similar structure (Lal et al., 1994).

ETYMOLOGY

The generic name refers to the hard incompressible texture.

Petrosaspongia nigra sp. nov. (Fig. 6A-C)

MATERIAL EXAMINED

HOLOTYPE: QMG 304685 ORSTOM (R1325). Stn. 133, Passe de Boulari, 22°29'07S, 166°26'00E, 12m. depth, 18 October 1981, Coll. P. Laboute.

PARATYPES: ORSTOM (R1320) Stn. 326, Récife d'Entre casteaux, Isle Huon, 18°08'40S, 162°49'50E, 38m., 26 August 1981, Coll. G. Bargibant. ORSTOM (R321) Stn. 196, Récife barrière M'Bere, 22°18'07S, 166°11'06E, 10-15m. depth, 9 November 1977, Coll. P. Laboute.

DIAGNOSIS

As for genus.

DESCRIPTION

Three specimens of this species were available in the ORSTOM collections and a further collection was made by the author. The sponge is massive spreading, with thick interlacing lobes arising from a spreading base. Individuals are large, covering an area of 50cm by 60cm and extending 20cm above the attachment base. Oscules are small, 1.0-2.5mm in diameter, flush with the surface, and scattered over the body. Colour in life is jet black externally, internally pale yellow ($rY^{7/4}$) to beige ($rY^{8/4}$), in spirit the same. The texture is hard, incompressible, and the surface has a brittle, rough aspect.

Surface. The surface is finely and evenly conulose. Conules are small, 0.2-0.3mm high, each with a fine projecting fibre rendering the surface rough to the touch.

Skeleton. The skeletal network is extremely dense, made up predominantly of tightly interlocking, strongly laminated, uncured secondary fibres. The arrangement is polygonal, irregular. Primary fibres are short, cored and arise only 800-1000µm below the surface when sectors of the secondary skeleton fuse to form a fenestrated spongin plate, from which primary elements extend to the surface. Primary fibres are 90-110µm in diameter. The predominant secondary fibres are 25-60µm in diameter, but some very fine

fibres 8-10µm in diameter occur, and in places almost constitute a tertiary network. The fine fibres do not occur throughout the skeleton. Considerable quantities of debris are scattered throughout the choanosome and along canals.

Soft tissue organisation. An ectosomal region 200-500µm deep is clearly set off from the choanosomal area. It is packed with pigment containing cells and has light, even collagen distribution. The choanosome has very light, even collagen deposition, choanocyte chambers are small, and spherical 20-25µm in diameter. Lacunae formed by subsurface canals can extend up to 1600µm below the surface membrane.

ETYMOLOGY

The species name describes the pigmentation of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Luffariella Thiele, 1899

TYPE SPECIES

Luffaria variabilis Polajaeff, 1884, by subsequent designation of Thiele (1899).

DIAGNOSTIC REMARKS

Thorectidae in which the cored primary and uncored secondary fibre reticulation is supplemented by a fine tertiary network. The sponges otherwise are similar to *Hyrrios* and *Cacospongia*, having a fine conulose unarmoured surface and simple non-fasciculate primary fibres. The branching pattern of the secondary and tertiary skeleton is complex.

Luffariella caliculata sp. nov.
(Fig. 7A-D)

MATERIAL EXAMINED

HOLOTYPE: QMG 304686 ORSTOM (R293) Stn. 195, East Coast, Goro, 22°16'80S, 167°05'10E, 50m depth, 3 Nov 1977. Coll. P. Laboute.

DIAGNOSIS

Shallow cup-shaped *Luffariella* with very limited coring material in the primary skeleton, fas-

culation of fibres near the surface and extremely fine tertiary fibres.

DESCRIPTION

A shallow cup shaped sponge, 14cm in diameter and 15cm high, arising from an attachment base 4.0cm in diameter. The body shape is regular, and the upper oscular surface is thrown into low undulations. Oscules are very evenly dispersed and are slightly depressed below the body surface. They are organised as oscular complexes with three to six exhalant canals opening to each one. The pale cream internal tissue (rY⁸/4) visible through each oscule contrasts with the golden brown external pigmentation (Y-R-Y⁶/4) and gives the sponge a characteristic speckled appearance. The texture is compressible and springy.

Surface. The surface is covered with fine low conules 0.5-1.0mm high on the lower, poral face; these are larger and less regular in arrangement on the upper oscular face.

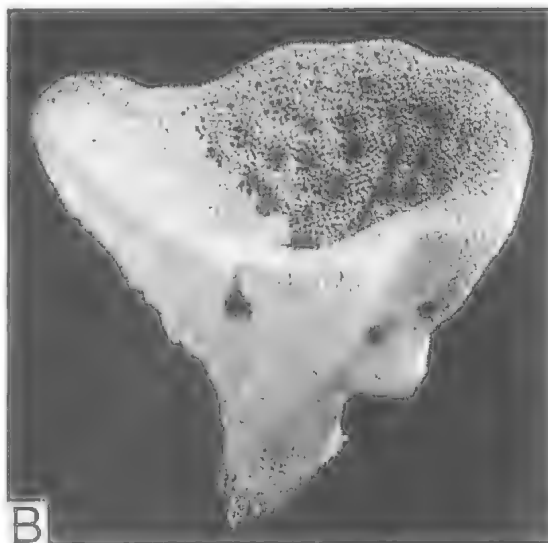
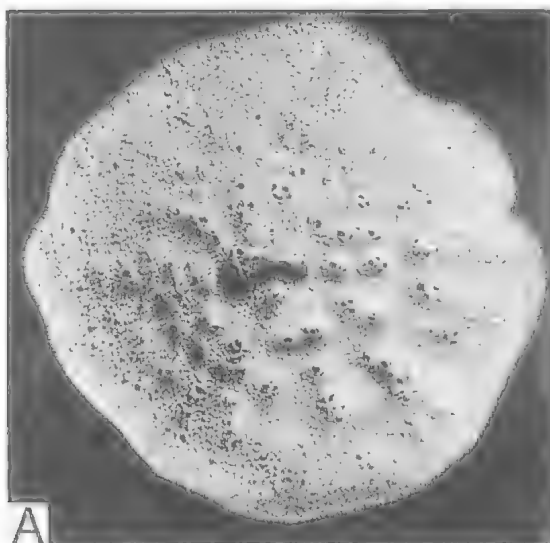
Skeleton. The skeleton is a regular, moderately dense network of primary fibres in which coring material is almost completely absent, only a few spicule fragments occurring. Near the surface the fibres attenuate to points and often divide to produce two or three terminal prongs. In the same region fibres can bifurcate and intertwine to produce short regions which are almost fasciculate. These features are also seen in the type species, *Luffariella variabilis* (holotype BMNH85.8.5.52). The secondary reticulum is quite regular approaching a rectangular arrangement, and is made up of uncured fibres. An extremely fine irregular tertiary fibre network is present. Primary fibres are 120-350µm in diameter, secondary fibres 10-50µm, and tertiary fibres 2-5µm in diameter.

Soft tissue organisation. A recognisable ectosomal region is present, it is 250-300µm deep, mainly occupied by large canals. The outer 80-100µm only is strongly collagen reinforced. The choanosome is only lightly infiltrated by collagen and choanocyte chambers are spherical, small and 15-25µm in diameter.

REMARKS

The growth form of the sponge, the paucity of coring material in the primary skeleton, the tendency to fasciculation of fibres near the surface,

FIG. 7. A-D, *Luffariella caliculata* sp. nov. A, Holotype QMG304686, apical view (x 0.3). B, Holotype QMG304686, side view (x 0.3). C, Photomicrograph showing primary fibres divided at the surface, secondary and tertiary fibres. (x 80). D, Photomicrograph showing detail of the tertiary network (x 200).



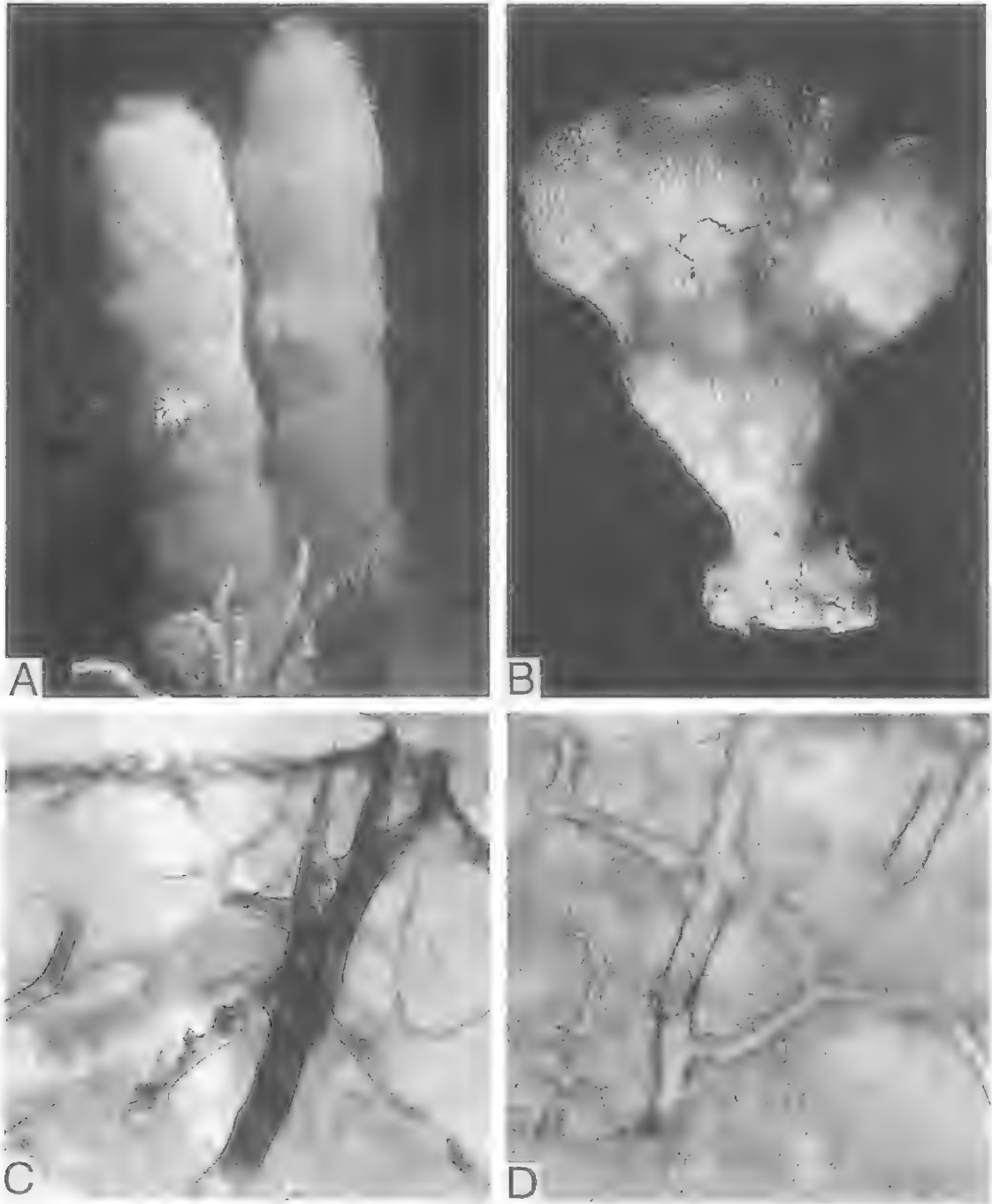


FIG. 8. A-D, *Luffariella cylindrica* sp. nov. A, Holotype QMG 304687, in situ (x 0.2). B, Paratype preserved specimen ORSTOM (R184) (x 0.5). C, Photomicrograph of primary fibres divided at the surface and secondary skeleton (x 80). D, Photomicrograph of secondary and tertiary network (x 200).

and the extremely fine tertiary fibres distinguish this sponge from other species of *Luffariella*. At present there are only two valid species of *Luffariella*, the type species *Luffariella variabilis* Poléjaeff recorded from the New Hebrides and Tahiti, and *L. geometrica* Kirkpatrick from Funafuti. The latter is a small cushion-shaped sponge with very regular skeleton, the former is massive or digitate with a dense skeleton. The genus is well characterised by the fine tertiary fibre network in conjunction with an unarmoured surface and simple, non-fasciculate primary fibres. The author has identified *L. variabilis* from Palau and Guam in addition to the type locality.

ETYMOLOGY

The specific name refers to the cup shape of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Luffariella cylindrica sp. nov.
(Fig. 8A-D)

MATERIAL EXAMINED

HOLOTYPE: QMG304867, ORSTOM (R1085) Stn. 114, Banc Gail, 22°22'04S, 166°39'02E, 35-38m depth, 29 Jun 1976. Coll. P. Bourret.

PARATYPE: ORSTOM (R184) Stn. 128, Passe de Dumbea, 22°22'04S, 166°15'40E, 30m depth, 13 Oct 1976.

DIAGNOSIS

Erect cylindrical *Luffariella* with primary fibres arranged in groups of 2 or 3 elements parallel to each other forming stout palisades.

DESCRIPTION

An erect, cylindrical sponge up to 60cm high and 8cm in diameter, arising from an attachment base 3.0-5.0cm wide. The body shape can be regular or thickened at intervals to form smooth lumps. There is a single large apical osculum 1.5-5cm in diameter which is served by many exhalant canal apertures which open to a cavity which extends the entire distance to the sponge base. A prominent membrane surrounds the osculum. It extends vertically for 1.0 cm and is supported by extensions of the primary fibres. The texture is compressible, but firm and springy, and the sponge exudes copious mucus when handled. Colour in life is gray (yY-R⁵/2), and in spirit the same.

Surface. The surface is covered with fine, evenly-spaced, low conules each supported by

several prongs of a primary fibre fascicle which tapers to a sharp point and projects above the surface membrane. There is no surface sand crust or cortex present.

Skeleton. The skeleton is an open network of lightly cored primary fibres, with clearly defined secondary and fine tertiary elements. Mesh arrangement is almost rectangular. The primary fibres are often arrayed in groups of two or three elements parallel to each other and connected by secondary fibres in a ladder-like array. The arrangement is not truly fasciculate, often split into two or three prongs at the surface. Primary fibres are 60-80µm in diameter, secondary fibres 20-30µm, and tertiary fibres 4-7µm in diameter. In the prominent oscular membrane, the primary fibres form stout palisades.

Soft tissue organisation. A distinct ectosomal region 250-350µm deep is marked by large canals separated by fine tissue tracts. The immediate subsurface region to a depth of 20-40µm is strongly infiltrated by collagen. The choanosome is only lightly reinforced by collagen and choanocyte chambers are spherical and small, 15-20µm in diameter.

REMARKS

Luffariella cylindrica is distinct from other species of the genus in its tubular habit and in the arrangement of the primary fibres.

ETYMOLOGY

The specific name refers to the cylindrical habit of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Fascaplysinopsis Bergquist, 1980

TYPE SPECIES

Aplysinopsis reticulata Hentschel, by original designation.

DIAGNOSTIC REMARKS

Thorectidae in which the primary fibres are fasciculate and cored with detritus. The secondary fibres are not cored, and branch in irregular fashion; they do not form a rectangular-meshed skeleton. Adjacent components of the primary fascicles are sometimes joined in ladder-like fashion, recalling the simple skeletal arrangement seen in *Thorecta* and *Thorectandra*. All fibres are very thick, with primary columns reaching 5.0mm and secondary connectives

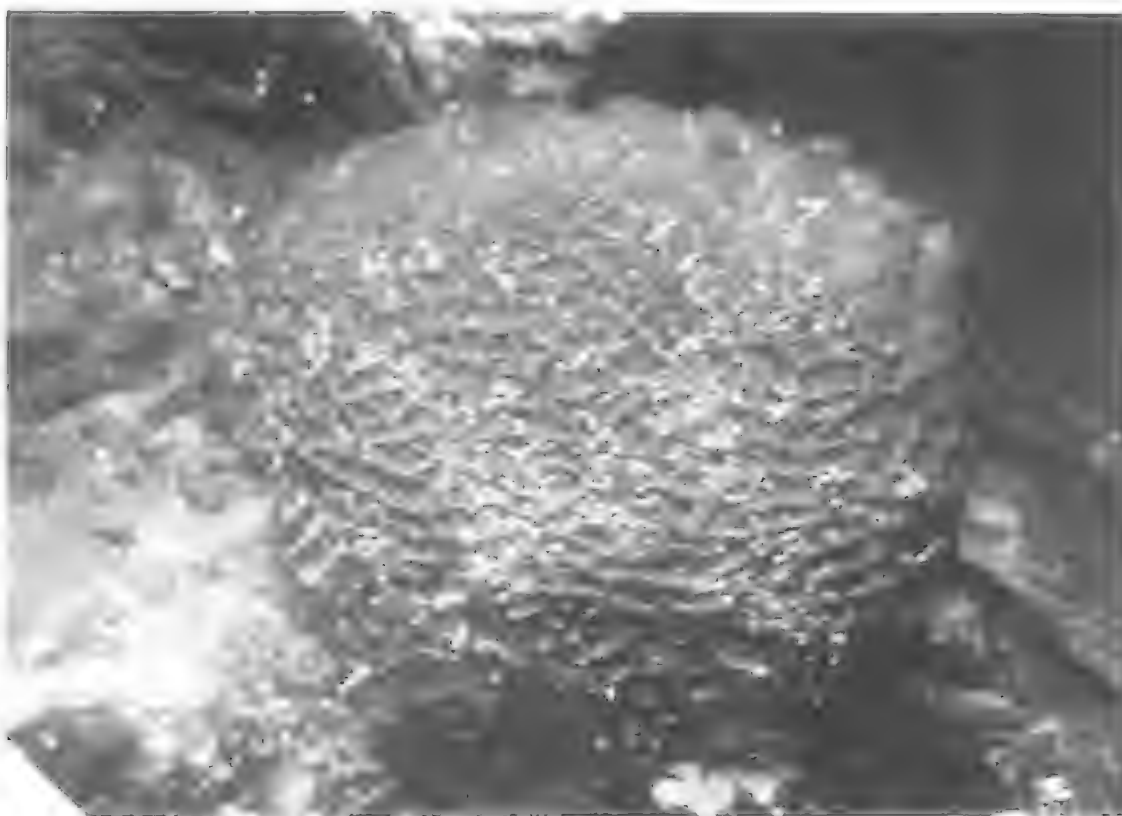


FIG. 9. *Fascaplysinois reticulata* (Hentschel) ORSTOM (R1344), in situ (x 0.5).

1.5mm. Pith is visible in all fibres. The sponge is cavernous but the texture in life is firm, and in alcohol hard, because of the coarse nature of the fibres. The surface is marked by prominent conules and a delicate superficial tracery of sand; there is no complete sand cortex. There is marked differential pigmentation, the surface being shiny black and the interior pale lemon yellow (Y^{8/8}). The gelatinous consistency of the matrix is a notable characteristic of the genus.

***Fascaplysinois reticulata* (Hentschel)
(Fig. 9)**

Aplysinopsis reticulata Hentschel 1912: 56, pl. xv(1), xvi (9).

MATERIAL EXAMINED

QMG304688, ORSTOM (R1344) Stn. 422, Iles Chesterfield, 20°58'10S, 158°34'60E, 40m depth, 21 Jul 1984. Coll. J. L. Menou.

REMARKS

The prominent surface tracery of conules and connecting ridges is well shown in this specimen.

DISTRIBUTION

Aru Island, Northern Great Barrier Reef, New Caledonia.

Family IRCINIIDAE Gray, 1867

Dictyoceratida in which the fibres making up the anastomosing skeleton are laminated in cross section and have a central pith region. These features are often obscured by the incorporation of large quantities of debris in the fibre skeleton and interstitially. The skeleton is irregular in arrangement and the primary fibres are always fasciculate, often forming very complex arrays. The secondary fibres are in general, uncured. A third element of the skeleton consists of fine collagenous filaments which are separate from the spongin fibre skeleton and which are dispersed in wavy to tangled tracts throughout the mesohyl.

Filaments have terminal knobs, are sometimes studded with lepidocrocyte granules and are made up of a collagen distinct from that found in the mesohyl matrix or in the fibres. The sponges are massive, lobate, spherical, digitate, cup shaped, encrusting always with a conulose surface except in forms which have an organised superficial sand crust, in which case the conules can be reduced to mammiform protruberences. The presence of the filaments renders the sponges very tough, almost impossible to tear. The choanocyte chambers are spherical and diploidal and the mesohyl, like that of the Spongiidae is only lightly infiltrated with collagen.

REMARKS

The family Irciniidae was established as Hirciniadae by Gray (1867), and used by Lendenfeld (1888) as Hircinidae. Since *Hircinia* is a synonym of *Ircinia* (Burton 1934) the family name Irciniidae applies. Bergquist (1978) established the family Thorectidae in a revision in 1980 and included *Ircinia* and allied genera in it. It has been noted, Bergquist and Wells (1983), that *Ircinia*, *Sarcotragus* and *Psammocinia* represented a distinct sub-group within that large assemblage. The evidence is sufficient to sustain separate family status, and that is formally done in this work (refer Thorectidae earlier).

Ircinia Nardo, 1833

Hircinia Nardo, 1834; *Stematumenia* Bowerbank, 1845; *Filifera* Lieberkuhn, 1859; *Polythersea* Duchassaing & Michelotti, 1864; *Euricinia* Lendenfeld, 1889.

TYPE SPECIES

Spongia fasciculata Pallas, 1766 *sensu* Schmidt (1862), by subsequent designation of de Laubenfels (1936).

DIAGNOSTIC REMARKS

Irciniidae in which primary fibres are cored with detritus and frequently attain great size by being woven into complex fascicles. Secondary fibres are simple and uncored. The matrix is charged with fine collagenous filaments. These are usually terminally knobbed, around 10-15µm in diameter, although thicker filaments have been recorded. The sponge surface is marked by prominent conules, and is unarmoured. In texture the sponge is extremely tough, and difficult to cut or tear.

Ircinia irregularis (Poléjaeff) (Fig. 10A, B)

Cacospongia irregularis Poléjaeff, 1884: 63, pl.vi, fig.10., pl. viii, fig.5.

Hircinia irregularis Burton, 1934: 578.

nec Hircinia gigantea Lendenfeld, 1889: 588, pl.xxvii, fig 7, pl.xxviii, fig.2, pl.xxxvi, figs. 1,6,10.

MATERIAL EXAMINED

HOLOTYPE: BMNH 85.8.8.37.

PARATYPES: ORSTOM (R166), Stn. 146, Ilot Sainte Marie, 22°17'08S, 166°29'02E, 9-15m depth, 7 Sept 1976. Coll. P. Bourret.

REMARKS

This species has been the subject of confusion since Lendenfeld merged it, in part, with his *Ircinia gigantea* from South Eastern Australia. Since Poléjaeff had only one specimen it is difficult to see how this action could be justified. *Ircinia irregularis* is the name which should be applied to the large, cushion shaped *Ircinias* with apical oscular clusters and strongly conulose surfaces which occur along the Great Barrier Reef, and extend to New Caledonia.

DISTRIBUTION

Torres Strait, Great Barrier Reef, New Caledonia.

Psammocinia Lendenfeld, 1889

TYPE SPECIES

Ircinia halmiformis Lendenfeld, 1889, by original designation.

Irciniidae which contain the fine interstitial filaments typical of *Ircinia* and *Sarcotragus* but which incorporate a large quantity of sand in fibres, matrix, and also as a thick superficial cortex. Many of the sand grains in the fibres are very large, coated individually with spongin and linked to the skeletal fibres by spongin strands. Fibres are only weakly fasciculate, and are often almost obscured by the accumulation of sand. Texture firm, sometimes brittle; the surface is either covered with rounded tubercles or pitted.

Psammocinia bulbosa sp. nov. (Fig. 11A-C)

MATERIAL EXAMINED

HOLOTYPE: QMG304689 ORSTOM (R1357), Stn.196, Récife barrière M'Bere, 22°18'07S, 166°11'06E, 10-75m depth, 9 Nov 1977. Coll. P. Laboute.

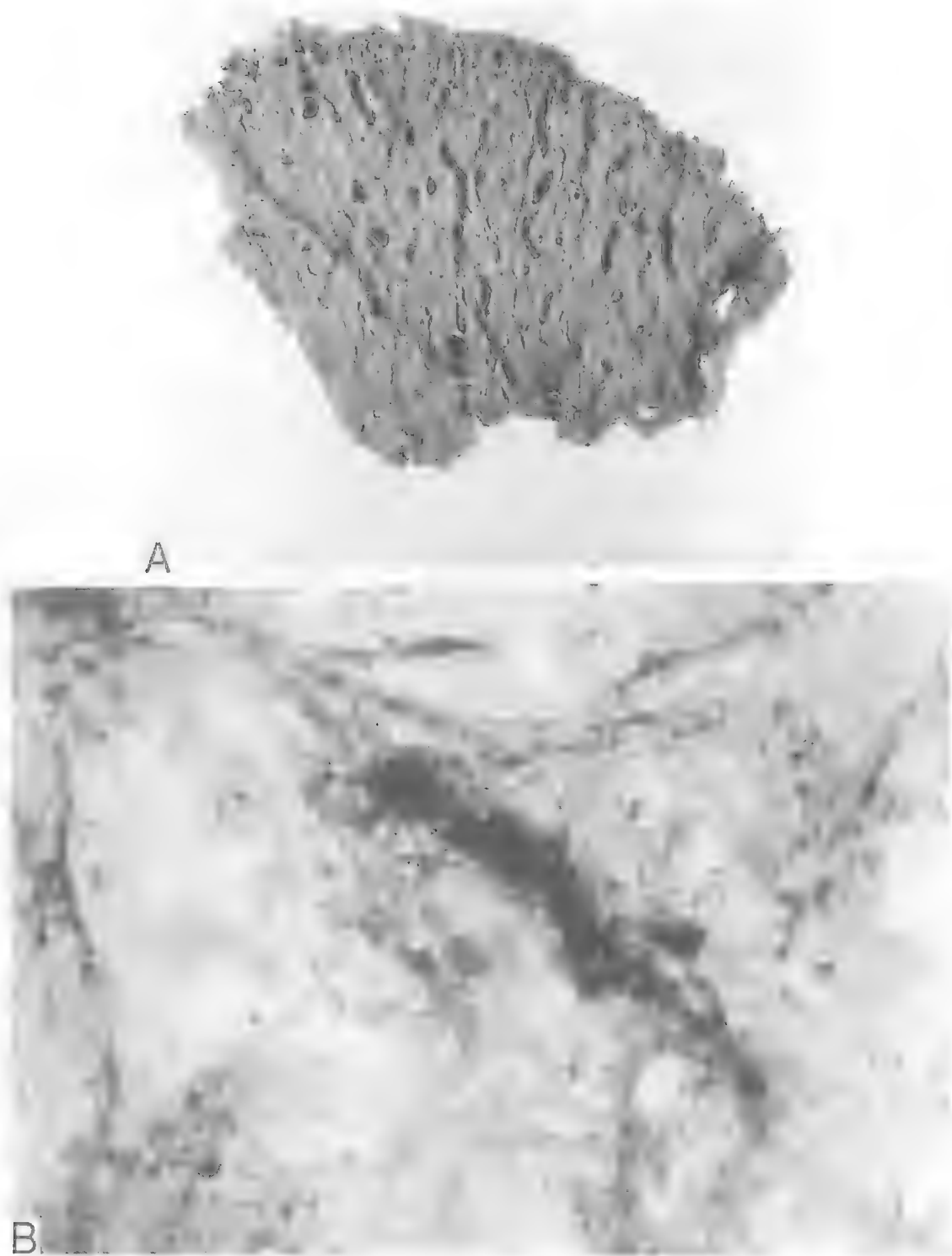


FIG. 10. A,B, *Ircinia irregularis* (Poléjaeff). A, ORSTOM (R166) vertical slice, preserved specimen (x 0.5). B, Photomicrograph showing primary and secondary skeleton (x 100).

OTHER MATERIAL: ORSTOM (R331, R393) Stn. 114, Banc Gail, 22°22'04 S., 166°39'02 E., 35-38m depth, 29 Jun 1976. Coll. P. Bourrel. ORSTOM (R573) Stn. 181, Ilot Maître, platier, 22°20'20S, 166°25'00E, 0.2-1.5m depth, 4 May 1977. Coll. P. Laboute. ORSTOM (R1273) Stn. 230, Passe de la Gazelle, 20°22'30S, 163°55'60 E., 12-50m depth, 30 Aug 1978. Coll. P. Laboute.

DIAGNOSIS

Massive repent *Psammocinia* with long oscular fistules and cored secondary fibres.

DESCRIPTION

The type specimen is a massive, repent sponge 20cm long, 3cm thick and 6cm wide, loosely attached to coral substrate. The body is in the form of a series of bulbous expansions from each of which one or two erect tapering oscular fistules arise. Osules are 2-5mm in diameter and are found flush with the surface as well as at the tip of the fistules. The texture is firm and crisp, just compressible and the colour in life is grayish white ($Y^{8/2}$) in spirit cream ($rY^{8/4}$).

Surface. The surface is covered with regularly spaced low conules 0.5-1mm high with rounded rather than pointed tips. A papery texture characterises the well developed sandy surface crust which is up to 1.0mm thick.

Skeleton. The skeleton is a loose irregular network of cored primary columns in which fibres twine, branch and interlock to make up stout fasciculate columns up to 700µm across. The secondary fibres are also irregularly arranged 30-50µm in diameter and are mainly cored, very few being clear of debris. The collagen filaments are very dense, fine, 3-5µm in diameter and terminated by spherical knobs. Debris extraneous to the fibres occurs only in the subdermal region.

Soft tissue organisation. The ectosomal region is made up of the sandy cortical crust which is up to 1mm deep, and an underlying region of lacunae formed by exhalant canals. Choanocyte chambers are spherical 20-30µm in diameter. Collagen deposition is light throughout the sponge.

REMARKS

Other species of *Psammocinia* are either cup shaped, encrusting or irregularly lamellate. *P. bulbosa* with its unusual shape, long oscular fistules and cored secondary fibres is quite dis-

tingent. No species have been described in the allied genera *Ircinia* and *Sarcotragus* which approach the present sponge in morphology.

ETYMOLOGY

The species name emphasises the bulbous body shape.

DISTRIBUTION

Known only from New Caledonia.

Family DYSIDEIDAE Gray, 1867

DIAGNOSTIC REMARKS

Dictyoceratida in which the spongin fibres making up the anastomosing skeleton are concentrically stratified to varying degrees. As in some members of the Irciniidae, this character is affected in development by the extent to which the sponge incorporates coarse detritus into the fibres. Pith components, as optically distinct central regions of the fibres, are evident except where fibres are detritus-packed. The choanocyte chambers are eurypylous, and the matrix contains only light collagen reinforcing. The sponges are histologically simple, with few secretory cell types present. The sponge texture is soft and compressible unless rendered brittle by interstitial detritus. Incorporation of debris into both fibres and matrix is frequent. The sponge surface is always conulose, but the size and arrangement of conules may range from very small, fine, and even (*Spongionella nigra*, *Dysidea herbacea*) to large and irregular (*Dysidea avara*).

Dysidea Johnston, 1842

Dysidea Johnston, 1842; *Dysidia* Agassiz, 1846; *Spongelia* Nardo, 1847; *Dysidea* Lieberkuhn, 1859; *Sarcocornea* Carter, 1859; *Halmopsis* Lendenfeld, 1885; *Haastia* Lendenfeld, 1889; *Dysidea* Delage, 1899

DIAGNOSIS

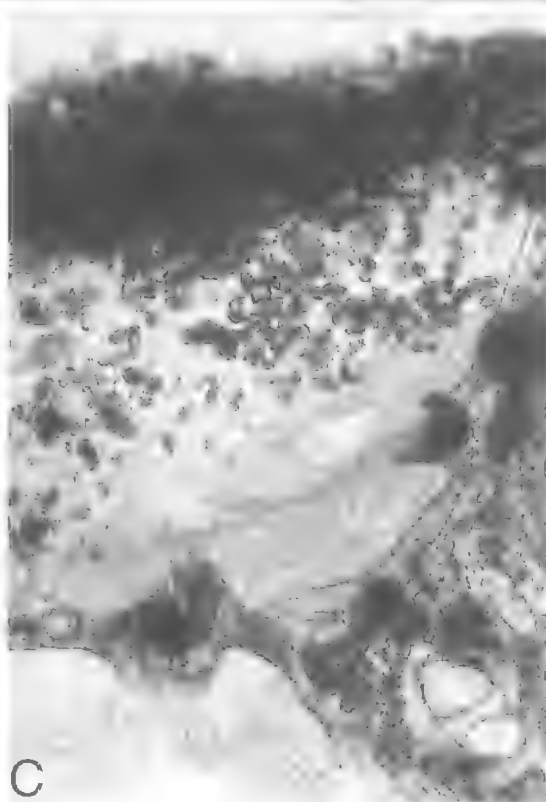
Dysideidae in which all fibres are filled with detritus.

TYPE SPECIES

Dysidea fragilis Montagu, 1814, by subsequent designation (Burton 1934).

overleaf

FIG. 11. A-C, *Psammocinia bulbosa* sp. nov. A, Holotype QMG304689, preserved specimen, side view (x 1.5). B, Holotype QMG304689, in situ (x 0.5). C, Photomicrograph of sand cortex and fasciculate skeletal elements (x 80).



Dysidea herbacea (Keller)

Spongelia herbacea Keller, 1889: 336, pl.20, Fig. 1.
Dysidea herbacea Bergquist, 1965: 140, Fig. 7a,b,c.

MATERIAL EXAMINED

ORSTOM (R158) Stn.198, Chenal des cinq milles,
 22°30'04S, 166°45'04E, 25-40m depth, 15 February
 1978. Coll. G. Bargibant.

REMARKS

This species is widespread throughout the Indo Pacific region and has a range of colour from gray green to green, and growth form from simple spreading mats with digitate or lamellate extensions to complex, soft, often interlocking lamellae.

The species has been confused with other *Dysidea* species, particularly *Dysidea chlorea* (de Laubenfels) and others yet to be described. The structure of the fibres (cf. Bergquist 1965, Fig. 7c) and the nature of the symbiotic cyanobacteria with which the sponge mesohyl is packed do not vary and serve to characterise *D. herbacea*.

DISTRIBUTION

Red Sea, Indian Ocean, Australia, Micronesia, Fiji.

***Dysidea arenaria* Bergquist**
 (Fig. 12)

Dysidea arenaria Bergquist, 1965: 144, Fig. 10 a, b.

MATERIAL EXAMINED

ORSTOM (R28, R30) Stn. 160, Ilot Maitre, 22°20'00S, 166°23'09E, 10m depth, 13 Oct 1976. Coll. P. Laboute. QMG 304690, 92-Ed-MI-10, 92-Ed-MI-14, Stn. 268, Ilot Maitre, 22°20'02S, 166°22'50E, 19m depth, 13 Oct 1992. Coll. C. Battershill.

REMARKS

This species is very common on the sandy substrate of subtidal *Halimeda* beds. It has been described and figured adequately by Bergquist (1965). The colour of the sponge in life can now be recorded as light gray (gY⁷/2) to pale mauve (bP⁸/2).

DISTRIBUTION

Palau Is, New Caledonia.

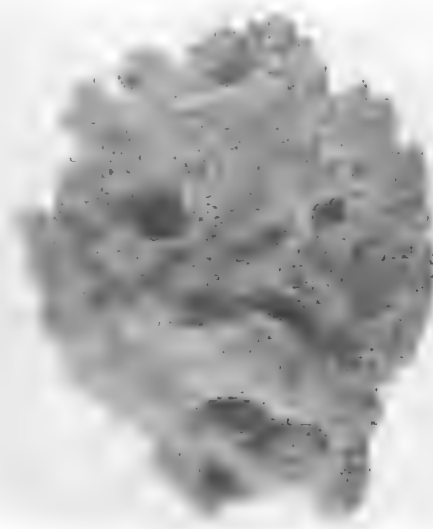


FIG. 12. *Dysidea arenaria* Bergquist, preserved specimen (x 2.0).

***Dysidea nigrescens* sp. nov.**
 (Fig. 13)

MATERIAL EXAMINED

HOLOTYPE: QMG304691 ORSTOM (R1252) Stn. 271, Entre L'ilot Téré and L'ilot Nda, 22°49'40S, 168°50'50E, 30m depth, 1 Apr 1980. Coll. P. Laboute.

DIAGNOSIS

Dysidea with a regular skeletal arrangement, low rounded conules and dark pigmentation throughout.

DESCRIPTION

A repent massive to lobate sponge 10cm long, 12cm wide and 3cm high loosely attached to coral rubble on a sandy lagoon bottom. Oscules are 2-5mm in diameter, situated apically on each lobe which arises from the sponge base. The texture is soft and friable and the sponge is easily torn. The colour is deep blackish purple in life (rP³/2) and cream in spirit (rY⁸/4).

Surface. The surface is very evenly covered with low rounded conules, 1mm high and wide, each of which is elevated by a single primary fibre. Between the conules the delicate dermal membrane is supported by a tracery of fine subdermal tracts. The apex of each conule is cream coloured where the sandy fibre content is exposed. This gives a very regular, light spotted appearance to the otherwise dark surface.



FIG. 13. *Dysidea nigrescens* sp. nov. Holotype QMG 304691, preserved specimen (x 2.0).

Skeleton. The skeleton is arranged on an almost perfect rectangular plan. The primary fibres are simple, not fasciculated and vary from 70 to 400µm in diameter, depending on the nature and extent of the debris incorporated. Secondary fibres are 40–100µm in diameter, always with some clear spongin visible around the coring material. The primary columns are spaced approximately 1 mm apart and the entire skeleton is thus a very fragile network.

Soft tissue organisation. The dermal membrane and ectosomal region are clear of debris and a well developed system of subdermal canals is present. The ectosomal region extends to a depth of 800µm and shows only traces of collagen deposition. The choanosome is lightly infiltrated with collagen and the mesohyl is filled with filamentous cyanobacteria. Choanocyte chambers are oval, eurypylous 120–180µm long and 50–80µm wide. No interstitial debris is present.

REMARKS

It is difficult to establish new species of *Dysidea* with certainty, particularly given the poor state of preservation of many type specimens and the very brief descriptions in the literature. This difficulty is compounded when the sponge does

not have a distinctive morphology as is the case for example in *Dysidea herbacea* or *Dysidea arenaria*. The combination of a very dark, almost black pigmentation throughout the sponge, the very regular skeleton, and low rounded surface conules suffices to distinguish *D. nigrescens* from others of similar morphology.

ETYMOLOGY

The species name refers to the dark colour.

DISTRIBUTION

Known only from New Caledonia.

Dysidea frondosa sp. nov.

(Fig. 14A–C)

MATERIAL EXAMINED

HOLOTYPE: QMG304692 ORSTOM (R1246) Stn. 124, Ilot Maitre, 22°20'08S, 166°25'05E, 24m depth, 26 Mar 1980. Coll. P. Laboute.

DIAGNOSIS

Dysidea with a frondose habit, pink-purple colour in life and irregular superficial fibre tracery.

DESCRIPTION

A repent sponge with multiple flattened lobate projections arising from a spreading base, it is 12 cm long, 8 cm high and 6 cm wide. Oscules are large, 3–6 mm in diameter, flush with the surface and scattered. The texture is soft, flexible, easily torn. The colour in life is pink-purple ($yR^5/2$) and in spirit dark brown ($yY-R^3/2$).

Surface. The surface is characterised by low, irregularly distributed conules 1–1.5 mm high, which have rounded or pointed tips. Sandy tracts running in the plane of the surface connect adjacent conules in some areas but not over the whole surface. These white tracts give an irregular web-like appearance to the surface.

Skeleton. All fibres are cored and it is not possible to distinguish between primary and secondary elements on the basis of size or orientation except in the immediate sub-surface area. The fibres are large, 120–400µm in diameter, heavily cored and strongly stratified, and make up an irregular network.

Soft tissue organisation. An ectosomal region 200–300µm deep is recognisable by the presence of exhalant canal lacunae and a denser superficial

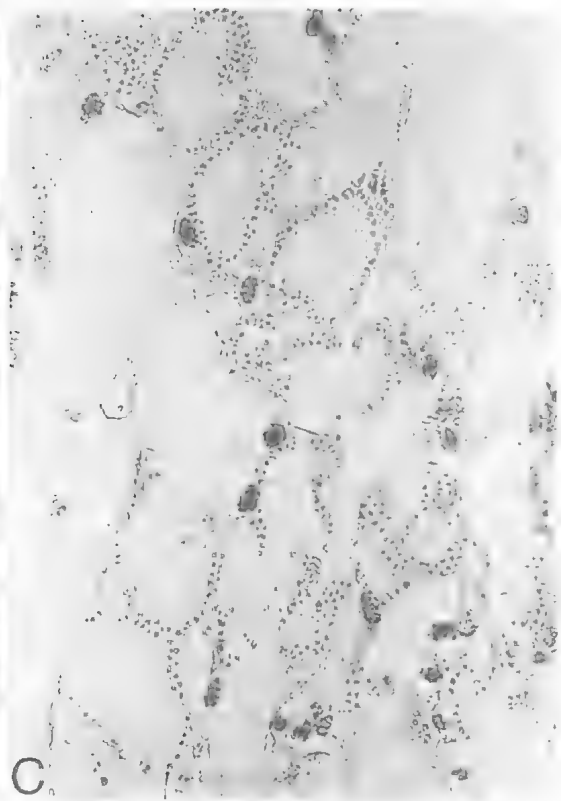
FIG. 14. A–C, *Dysidea frondosa* sp. nov. A, Holotype QMG304692, preserved specimen (x 1.0). B, Photomicrograph of choanosome and a portion of the fibre skeleton (x 100). C, Photomicrograph showing choanocyte chambers and scattered pigment cells (x 300).



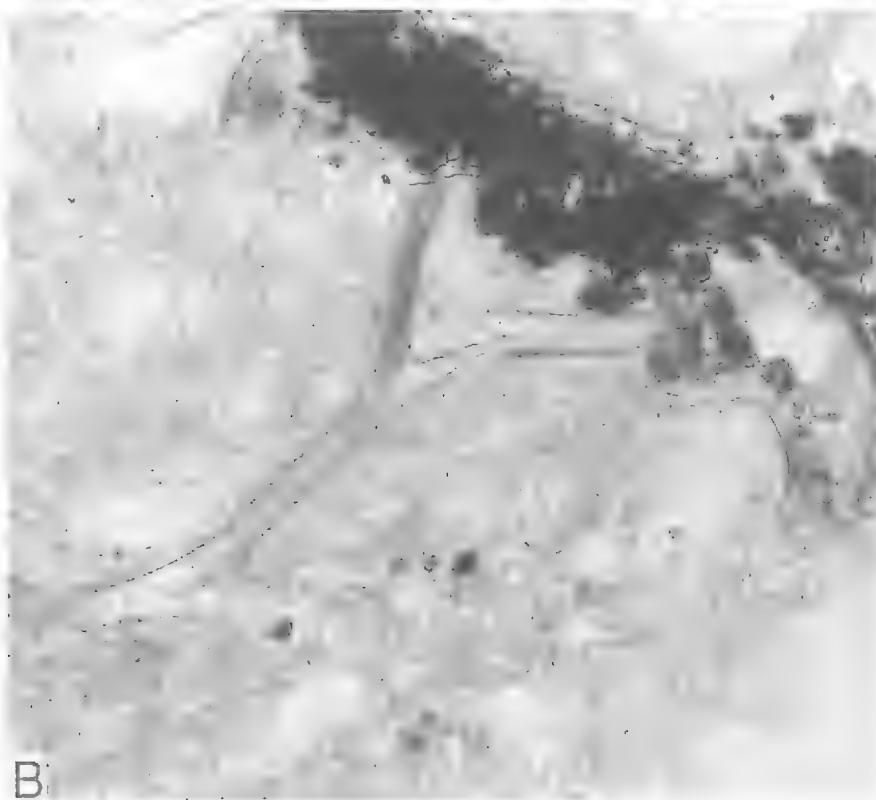
A



B



C



region 30–40 µm deep of light collagen reinforcement. The choanosome has negligible collagen deposition and low mesohyl content, most volume being occupied by the oval eurypylous choanocyte chambers 50–80 µm in maximum dimension, and canals. All areas of the sponge contain numerous dark brown pigmented cells. There is no interstitial debris.

REMARKS

The frondose habit in conjunction with the colour and prominent irregular, superficial fibre tracery distinguish this species from others in *Dysidea*.

ETYMOLOGY

The species name refers to the frondose habit of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Euryspongia Row, 1911

DIAGNOSTIC REMARKS

Dysideidae in which the primary fibres are cored and the secondaries are clear of debris. The primary network is regular, the secondary is branching. The surface is usually marked by a very delicate superficial network extending between conules and pore areas.

TYPE SPECIES

Euryspongia lactea Row, 1911, by monotypy.

Euryspongia delicatula sp. nov.
(Fig. 15A,B)

MATERIAL EXAMINED

HOLOTYPE: QMG304693, ORSTOM (R1225) Stn. 184, Ilot Ue, 22°42'07S, 166°49'00E, 25m depth, 8 Jun 1977. Coll. P. Laboute.

DIAGNOSIS

Euryspongia having bright violet colour, low rounded conules, and a fasciculate primary skeleton.

DESCRIPTION

A massive sponge, 18cm long, 10cm wide and 8cm high, growing on coral from a broad attachment base. Oscules are 2–6mm in diameter, flush

with the surface, solitary or aggregated in groups and dispersed over the entire surface. The texture is spongy, very compressible but tough. The colour in life is violet (PR-P⁵/8) throughout, in spirit brown, the colour of spongin fibre (Y-R-Y⁶/6).

Surface. The surface is characterised by evenly spaced rounded conules, 1–3mm high, elevated by single or multiple primary fibres. Between the conules fine subdermal tracts radiate under the fine dermal membrane and confer the cobweb-like appearance on the surface as noted in other *Euryspongia* species.

Skeleton. The skeleton is made up of cored primary fibres, which become strongly fasciculate in the immediate sub-surface region, and a loose, irregularly disposed network of clear secondary fibres. Primary fibres are 200–400 µm in diameter, secondary fibres 50–120 µm in diameter. All fibres are strongly stratified and a clear pith region is present, but is most evident in the uncored secondary elements. A small amount of interstitial debris is scattered throughout the body.

Soft tissue organisation. An ectosomal region 150–250 µm deep is made up of subdermal lacunae overlain by a collagen reinforced region 60–80 µm in extent. The choanosome has very light collagen deposition in the sparse mesohyl. It is made up largely of oval eurypylous choanocyte chambers, 80–120 µm in greatest dimension, and of canals.

REMARKS

The brilliant violet colour, low rounded conules and fasciculate primary skeleton are the major features distinguishing this species from other species of *Euryspongia*, many of which are to date poorly described. Examination of the type species, *Euryspongia lactea* Row, from the Red Sea shows that the sponge is not like *Spongia* in skeletal characteristics as Row suggested. It has clearly stratified fibres with an evident pith and primary fibres with some fasciculation.

ETYMOLOGY

The species name refers to the delicate appearance of the sponge surface.

DISTRIBUTION

Known only from New Caledonia.

FIG. 15. A-B, *Euryspongia delicatula* sp. nov. A, Holotype QMG304693, in situ (x 0.5). B, Photomicrograph showing primary and secondary fibres (x 100).

***Euryspongia vasiformis* sp. nov.**
(Fig. 16A, B)

MATERIAL EXAMINED

HOLOTYPE: QMG304694 ORSTOM (R812) Stn. 109, Baie de Citrons, 22°18'30S, 166°25'50E, 8-10m depth, 31 Mar 1978. Coll. G. Bargibant.

PARATYPE: ORSTOM (R1282) Stn. 383, Recife Toombo, Pente externe, 22°23'00S, 166°26'30E, 20-30m depth, 28 Apr 1981. Coll. P. Laboute.

DIAGNOSIS

Thin walled vase-like *Euryspongia* having an irregular disposition of the primary skeleton.

DESCRIPTION

An irregular cup shaped sponge 16cm high, 10cm in apical diameter with walls 4-8mm thick, growing attached to worm tubes and coral rubble on sandy *Halimeda* flats. Oscules are small, flush with the surface and scattered on both interior and exterior faces of the sponge. The texture is soft, flexible, easily torn. The colour in life is dark brown, (yY-R¹/2) in spirit identical.

Surface. Both interior and exterior surfaces are covered with closely spaced sharp conules 1-2m high, each supported by a single primary fibre. A prominent tracery of surface tracts connects adjacent conules and confers a web-like appearance on the surface. (See Bergquist 1980: fig. 19 a,b,d).

Skeleton. The skeleton is made up of lightly cored primary fibres which can be slightly fasciculate near the surface, and a loose open reticulum of uncored secondary fibres. The thin walled construction of the sponge influences the disposition of the primary tracts which often are disposed parallel to the surface before converging toward the conules. Primary fibres are 80-200µm in diameter, secondaries 40-120µm in diameter and all are markedly stratified. No interstitial debris is present.

Soft tissue organisation. An ectosomal region, 150-300µm deep is made up of subdermal canals overlain by a superficial, collagen reinforced layer 30-50µm deep. There is no evident collagen deposition in the choanosome, the volume being largely taken up by oval eurypylous choanocyte chambers, 60-90µm in maximum dimension, and by canals.

REMARKS

The thin walled vase-like construction of the sponge and the irregular disposition of the primary skeleton differentiate *E. vasiformis* from other species of *Euryspongia*.

ETYMOLOGY

The species name emphasises the vasiform shape of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Order DENDROCERATIDA Minchin, 1900

DIAGNOSTIC REMARKS

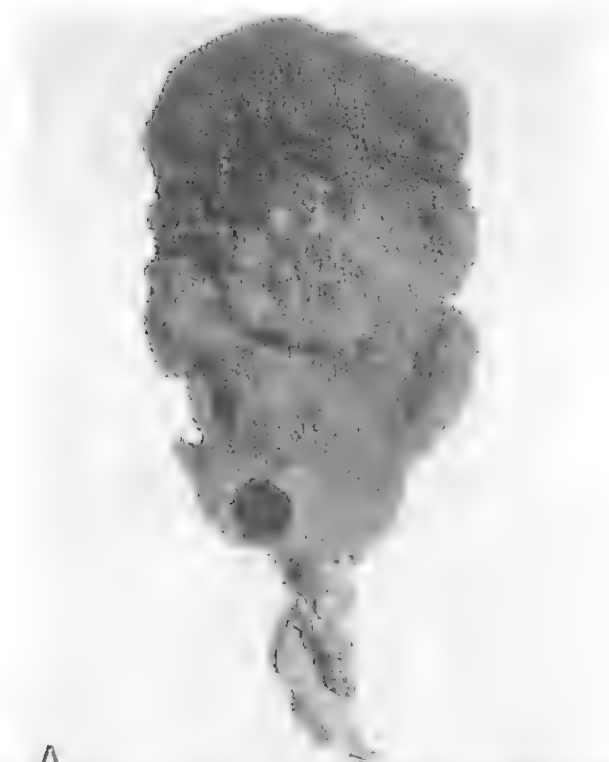
Ceratinomorpha in which the fibre skeleton, though usually present, is reduced in relation to soft tissue and is entirely absent in one genus. The skeleton arises from a continuous spreading basal plate, and adopts either a dendritic or an anastomosing pattern. In anastomosing forms there is never any clear size distinction between primary and secondary elements. The fibres are always pithed and strongly laminated, usually quite stout, and frequently incorporate recognisable cellular (spongocyte) elements. Free fibrous spicules may occur in addition to the main skeleton. The choanocyte chambers are large and sac-like or tubular, elongate, and branched; matrix volume is low in relation to chamber and canal volume, and the matrix is only weakly infiltrated by collagen. This, in conjunction with the generally reduced fibre skeleton, makes the sponges soft and fragile. The pith in the fibres is markedly distinct from the bark elements, and in structure is close to that seen in the Verongida. It is common to find dark fibre pigmentation contrasting with the matrix pigmentation, which is always uniform throughout the sponge. Larvae are either large, incubated parenchymellae with complex structure and histology and always with a terminal clump of long cilia or (in one family) simple parenchymellae lacking terminal long cilia.

Family DARWINELLIDAE Merejkowsky, 1879

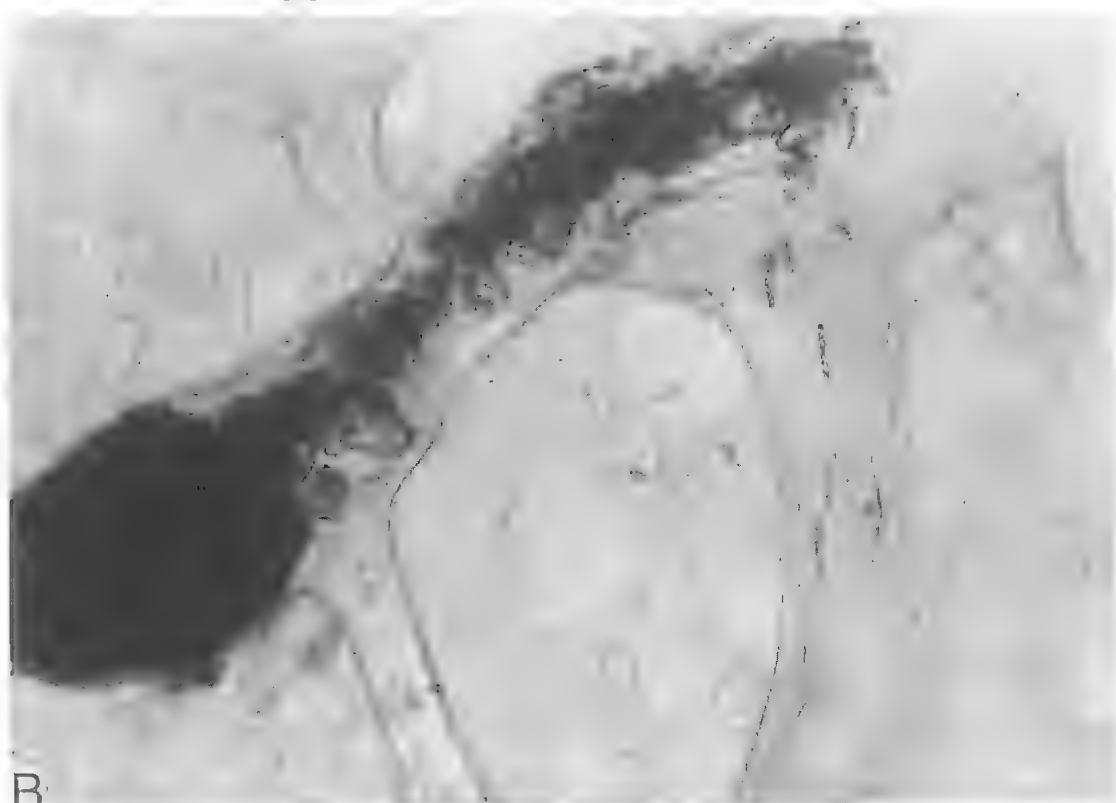
DIAGNOSTIC REMARKS

Dendroceratida in which the fibrous skeleton, where present, is completely dendritic and sometimes supplemented by spongin spicules which

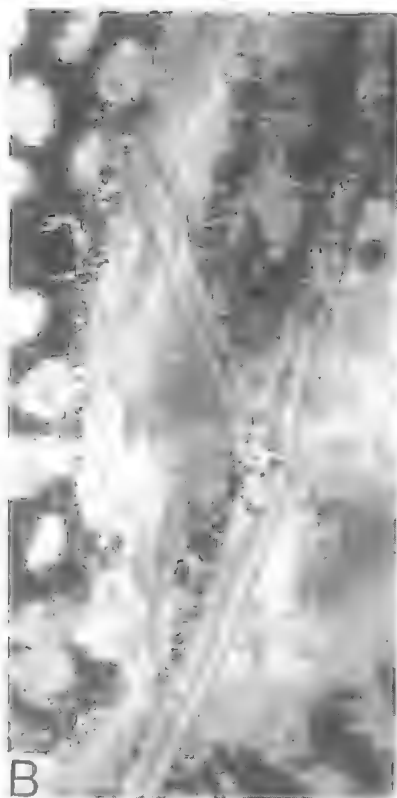
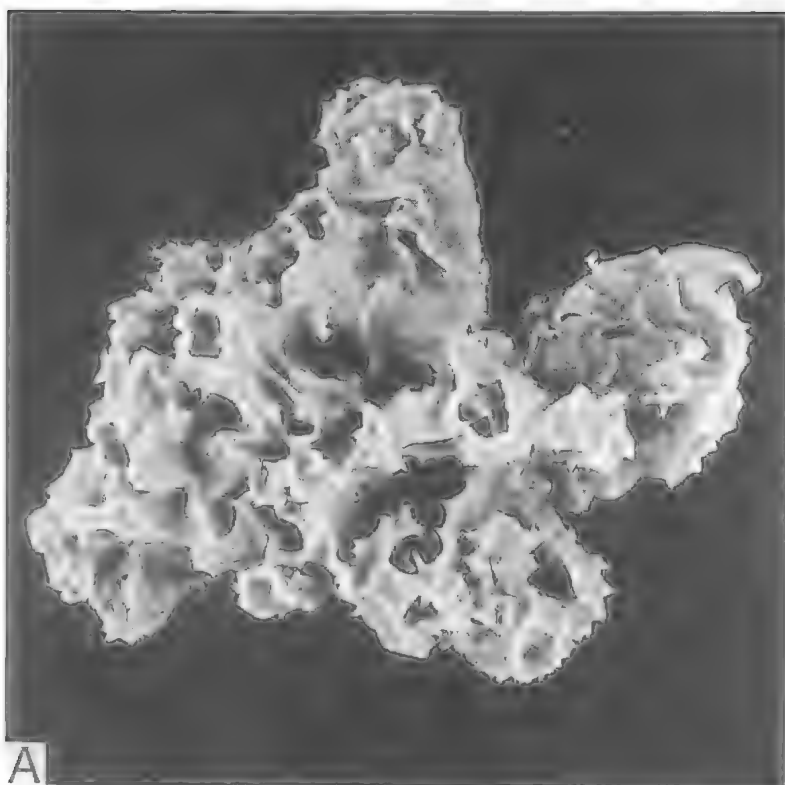
FIG. 16. A-B, *Euryspongia vasiformis* sp. nov. A, Holotype QMG 304694, preserved specimen (x 0.5). B, Photomicrograph showing choanosome and primary and secondary fibres (x 100).



A



B



are not attached to the primary skeleton. Species are frequently encrusting but where massive or erect, their fibrous skeleton, like that of the encrusting forms, always arises from a flat basal spongin plate. The fibres are comparable to those of the Verongida in structure, with a laminated bark surrounding a central, markedly distinct pith. The pith can be partially replaced by coring material. As better descriptions of sponges belonging to this group have appeared, it has become clear that the family is cohesive and that the senior name Darwinellidae can be applied. This usage is well documented by Hooper and Wiedenmayer (1994).

Chelonaplysilla de Laubenfels, 1948

TYPE SPECIES

Chelonaplysilla narvus (Carter, 1876) by original designation.

DIAGNOSTIC REMARKS

Darwinellidae which have a separable cortex reinforced by a delicate reticulum of sand grains. Fibre structure is like that of *Aplysilla*, but in some species that become erect and branching, the supporting skeleton becomes branched.

Chelonaplysilla aurea sp. nov. (Fig. 17A-C)

MATERIAL EXAMINED

HOLOTYPE: QMG304695, ORSTOM (R1349), Stn. 423, Iles Chesterfield, 20°58'10S, 158°34'60E, 42-44m depth, 23 Jul 1984. Coll. G. Bargibant.

DIAGNOSIS

Chelonaplysilla with a golden yellow colour in life, large pointed conules and large oscules which are flush to the surface and distributed over the whole body.

DESCRIPTION

A soft spreading sponge, 6cm by 8cm in area and 2cm thick. Oscules are large, 3-6mm in diameter, flush with the surface and distributed over the whole body. The texture is soft, collapsible, easily torn. The colour in life is golden yellow (Y-R-Y⁷/10) and in spirit pale pink (rY-R⁶/4).

Surface. The surface is covered with large pointed conules, 1-2mm high which are often supported by two primary fibres giving a tent-like appearance to each one. An organised and beautifully regular, sandy reticulum occurs over the entire surface. Meshes of the reticulum are oval, 100-150µm in maximum dimension.

Skeleton. The skeleton is dendritic, made up of sparsely distributed clear fibres with the pithed, laminate construction typical of the family. Fibres are uncured, 110-140µm in diameter near the surface, up to 200µm in diameter basally. All fibres incorporate some cellular elements.

Soft tissue organisation. The ectosomal region, apart from the superficial sandy crust, shows very little differentiation. It is lightly reinforced with collagen to a depth of 30-40µm. Prominent ectosomal lacunae occur beneath each osculum, but otherwise the ectosome is not strongly set off from the underlying choanosome. The choanosome is composed largely of oval eurypylous choanocyte chambers, 110-180µm in maximum dimension, and canals. Mesohyl volume is greatly reduced.

REMARKS

The pigmentation, oscular and conule structure differentiate the species from others described in *Chelonaplysilla*.

ETYMOLOGY

The species name refers to the brilliant colour.

DISTRIBUTION

Known only from the Chesterfield Islands.

Darwinella Muller, 1865

Darwinia Schultze, 1865

TYPE SPECIES

Darwinella mulleri Schultze, 1865, by monotypy.

DIAGNOSIS

Darwinellidae in which the slightly ramified, dendritic fibre skeleton is supplemented by diactinal, triactinal or quadriactinal spongin spicules. There is no sand in the fibres. The sponges are encrusting or massive to lobate.

FIG. 17. A-C, *Chelonaplysilla aurea* sp. nov. A, Holotype QMG 304695, preserved specimen (x 1.0). B, Photomicrograph showing the structured surface crust and a portion of the fibre skeleton (x 80). C, Holotype QMG304695, in situ, (x 2.5).

***Darwinella* sp. cf. *intermedia* Topsent**
(Fig. 18A, B)

MATERIAL EXAMINED

QMG304696, ORSTOM (R348) Stn. 114, Banc Gail, 22°22'04S, 166°39'02E, 35–38m depth, 29 Jun 1976. Coll. P. Bourret. QMG 304697, ORSTOM (R1294), Stn. 305, Ile Paaba, 19°55'30S, 161°37'25E, 27m depth, 24 Jun 1981. Coll. P. Laboute.

REMARKS

There is great confusion in the literature with respect to the species of *Darwinella*. Excellent reviews by Topsent (1905) and Pronzato (1975) have been negated by later assertions that colour was widely variable within species (Pulitzer-Finali and Pronzato, 1980). This was seized upon by Wiedenmayer (1989) as an opportunity to refer clearly diverse sponges of a range of colours to two Southern Hemisphere species, *D. gardineri* with free oxete spicules, and *D. australiensis* with triactinal to polyactinal spicules of a range of sizes. Bergquist et al (1990b), in a paper concentrating on diterpene chemistry, drew attention to the existence of several *Darwinella* species from Australia and New Zealand based upon terpene profiles, colour and spicule size and morphology. Poiner and Taylor (1990) gave a very sketchy description of one of these Australian species. The brilliant golden orange *Darwinella* referred to by Bergquist et al was recorded by those authors as *Aplysilla tango*. Although not mentioned in the description, this sponge has abundant, short, wavy oxete fibrous spicules and is a *Darwinella*. Specimens of this sponge were among those lumped into *D. gardineri* by Wiedenmayer.

Also included in Wiedenmayer's melange were yellow specimens with long rayed triactinal spicules. These are possibly identical to the present specimens from New Caledonia; this remains to be confirmed. The closest species in the literature to these yellow *Darwinellas* with triradiate spicules is *D. intermedia* Topsent from Banyuls, but the two are almost certainly not identical. The New Caledonian specimens are undoubtedly new, but the material available at present is not adequate on which to base a new species description. Consequently the sponge is simply compared to *D. intermedia* which itself needs redescription.

Bergquist (1994 in press) has a full discussion of the Australasian species of *Darwinella* based on consideration of morphological, histological and chemical characters. There is no described species from that region into which the present

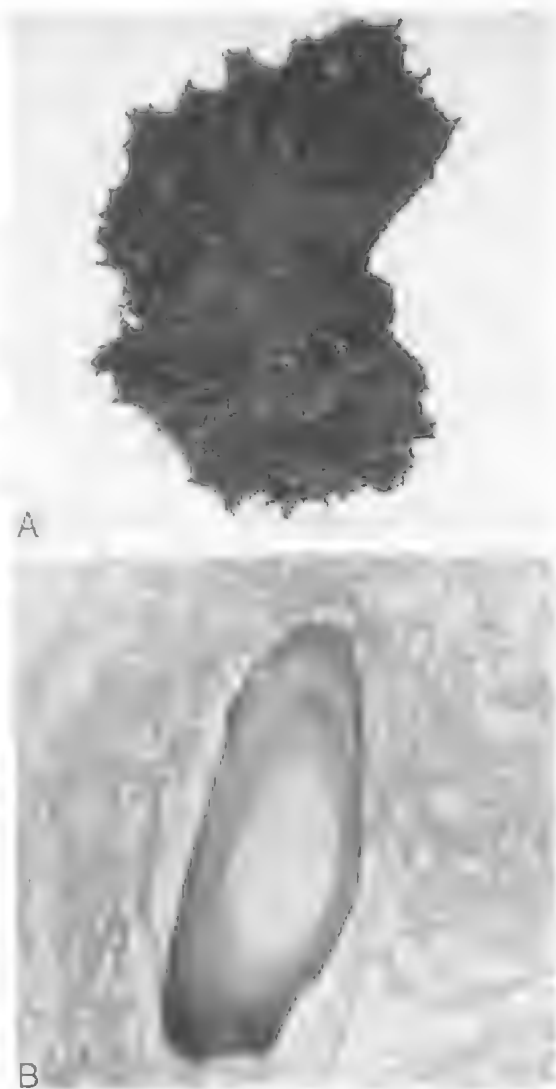


FIG. 18. A-B, *Darwinella* sp. cf. *intermedia* Topsent. A, ORSTOM (R348), preserved specimen (x 0.75). B, Photomicrograph of fibre in cross section (x 75).

specimens fit. Their colour is greenish yellow to yellow ($rY^8/10$) in life, dark purple black ($rR-P^2/2$) in spirit, and the fibre spicules are moderately rare triradiates.

***Dendrilla* Lendenfeld, 1883**

TYPE SPECIES

Dendrilla rosea Lendenfeld, 1883, by subsequent designation (Topsent, 1905).

DIAGNOSIS

Large, erect, branching or complex lamellate Darwinellidae in which the fibres branch repeatedly but do not anastomose. The fibres contain no coring material.

Dendrilla rosea Lendenfeld
(Fig. 19A, B)

Dendrilla rosea Lendenfeld, 1883: 271-294, pl. 10, figs. 3, 4; pl. 12, figs. 16, 19-23; pl. 13, figs. 24-27, 29-32; Lendenfeld, 1889: 716-719, pl. 44, figs. 4, 7, 8, 11; pl. 45, figs. 3, 4, 7, 8, 9; Bergquist, 1980: 486; Bergquist & Skinner, 1982: 49, pl. 1, fig. 3 (colour); Bergquist, in press.

Dendrilla cactus Selenka (sensu Wiedenmayer only), 1989: 152, fig. 98.

nec. *Spongelia cactus* Selenka, 1867: 566, pl. 35, fig. 5.

MATERIAL EXAMINED

ORSTOM (R121b), Stn. 136, 22°00'07S, 165°56'04E, Ilot Canard, 20m depth, 1 Oct 1991. Coll. G. Bargibant.

REMARKS

Bergquist (in press) gives a full discussion of the confusion in nomenclature surrounding this species, and holds open the possibility that spiky, erect, terete forms from New Zealand and Australia, presently placed within *D. rosea* may require a new name. Further Australian collections are required to resolve this, since Wiedenmayer's analysis (1989) cannot be seriously regarded. Regardless of this possibility the fleshy, lobose rose-red forms of *Dendrilla* will retain the name *Dendrilla rosea*. The only feature in which the single New Caledonian specimen differs from New Zealand and Australian specimens is that the laminations of the fibres are slightly twisted like a skein of wool, rather than being parallel to the long axis of the fibre.

DISTRIBUTION

New Zealand, Southern Australia, New Caledonia.

Family DICTYODENDRILLIDAE
Bergquist, 1980

DIAGNOSTIC REMARKS

Dendroceratida in which the skeleton is reticulate and the fibres are concentrically laminated and pithed. Pith may be substantially obscured by incorporation of detritus into fibres. Fibre skeleton can be augmented by the addition of free spongin spicules. The large, oval choanocyte chambers are eurypylous. The reticulate structure of the skeleton allows these sponges to attain large size despite the delicate, cavernous nature of the soft tissue. The fibre colour is frequently dark purple, red, or black, and contrasts with the soft tissue which is either pale or densely and uniformly pigmented.

Acanthodendrilla gen. nov.

TYPE SPECIES

Acanthodendrilla australis sp. nov.

DIAGNOSIS

Dictyodendrillidae in which the reticulate fibrous skeleton has irregular mesh arrangement with all elements cored with detritus. Reticulation is more pronounced superficially, and ascending, primary fibres project above the sponge surface. The strongly cored fibres and irregular reticulum distinguish the genus from *Dictyodendrilla* and the absence of free fibrous spicules distinguishes it from *Igernella*.

Acanthodendrilla australis sp. nov.
(Fig. 20A-C)

DIAGNOSIS

As for genus

MATERIAL EXAMINED

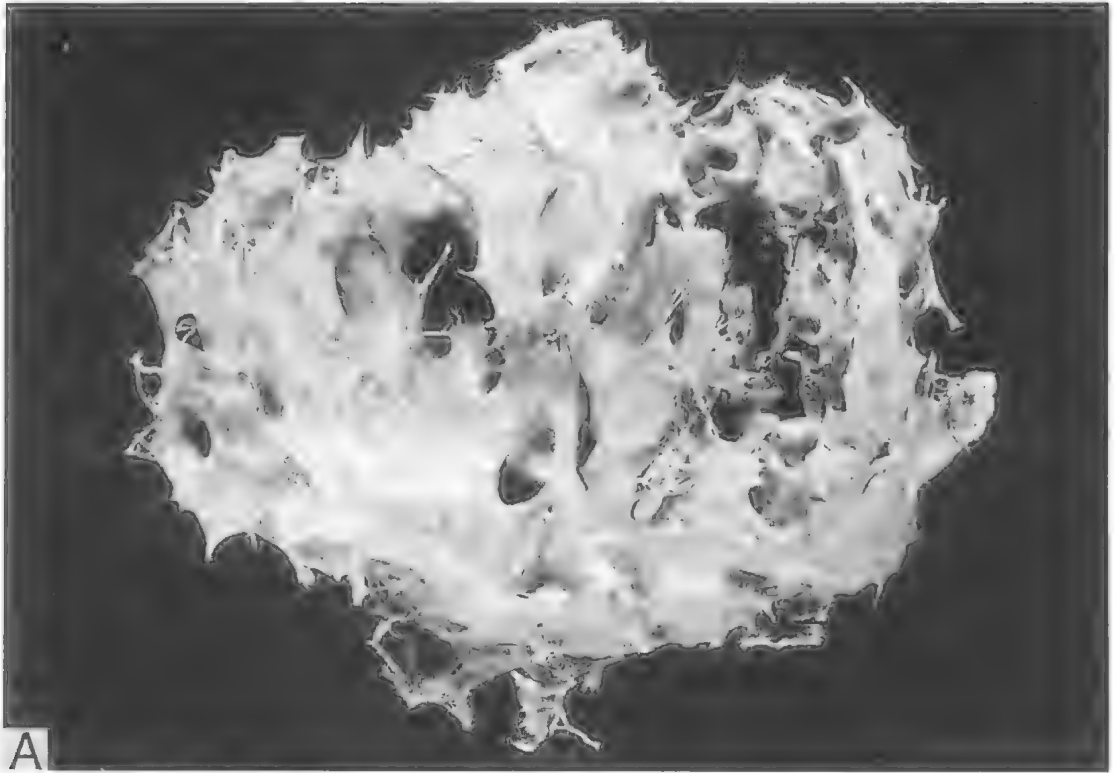
HOLOTYPE: QMG304698, ORSTOM (R121a), St. 136, Ilot Canard, 22°19'02S, 166°21'07E, 20m depth, 16 Apr 1981. Coll. P. Laboute.

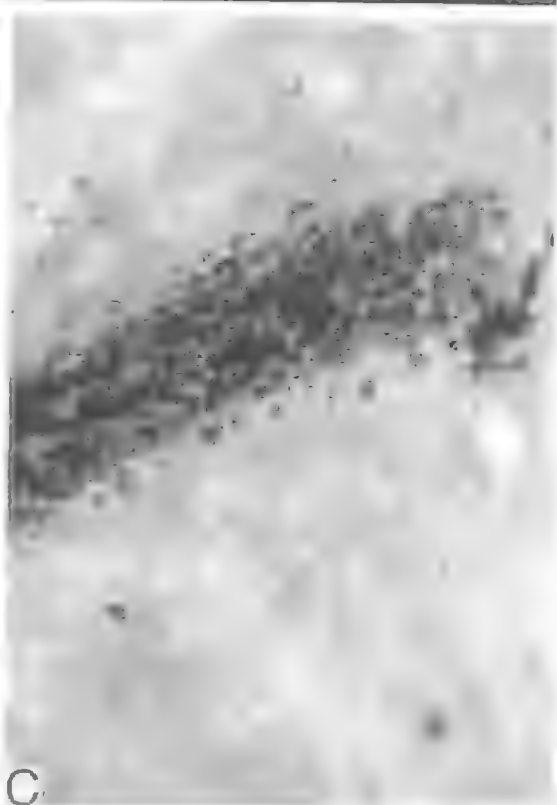
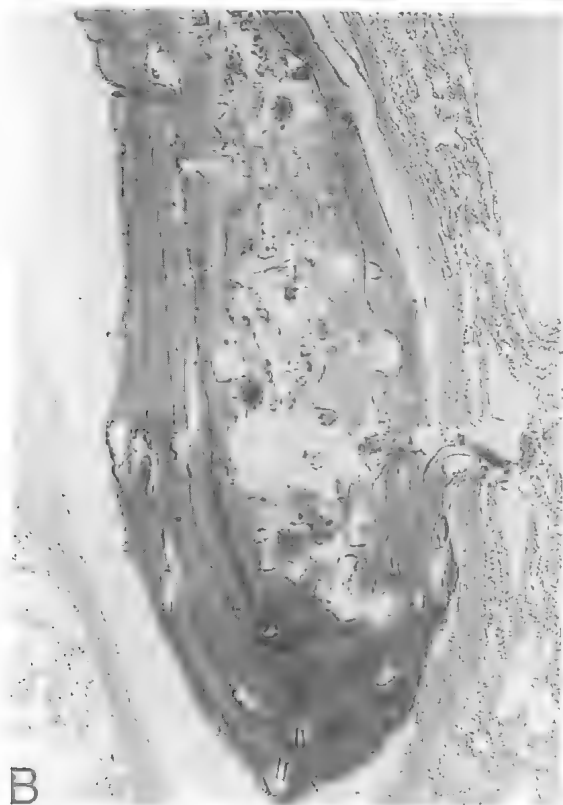
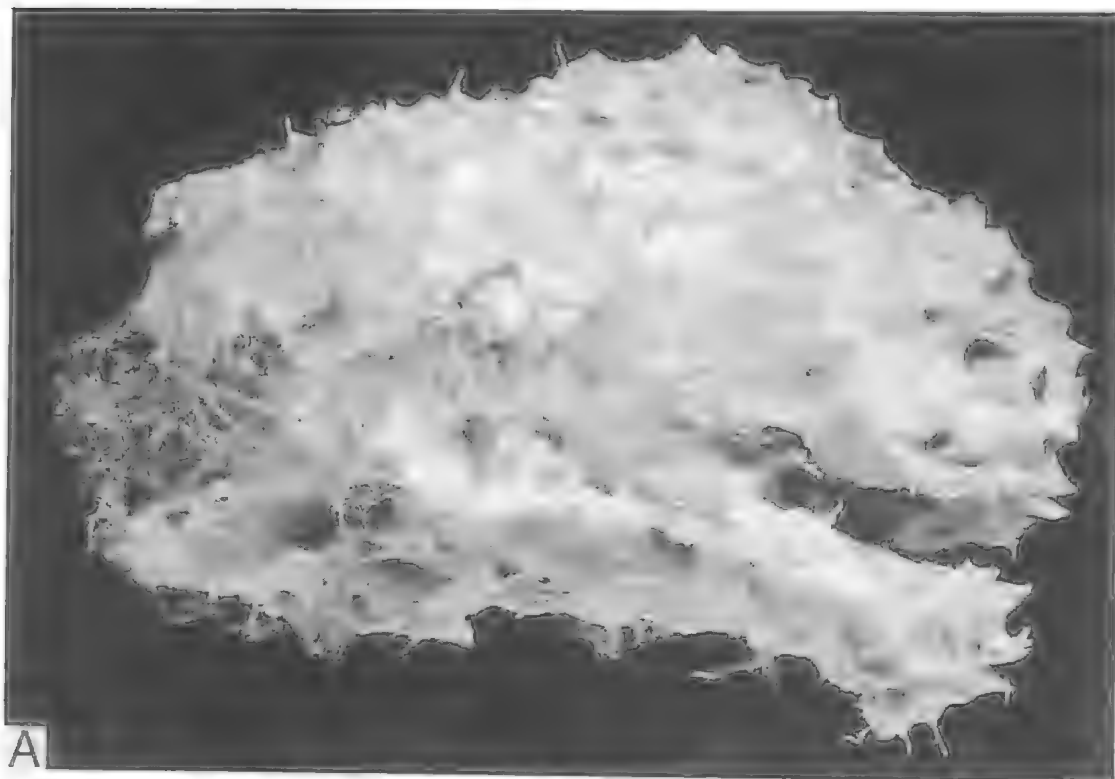
DESCRIPTION

The body is in the shape of a thick fan rising from a broad attachment base. The sponge is 11.0cm high, 13cm wide, and 4.5cm thick. Oscules are irregularly disposed but confined to the broad upper surface of the body. They are large

overleaf

FIG. 19. A, B, *Dendrilla rosea* Lendenfeld. A, ORSTOM (R121b), preserved specimen (x 1.0). B, Photomicrograph of fibre showing lamination pattern (x 100).





0.2 to 1 cm in maximum dimension. Colour in life is unknown, in spirit biscuit (Y-R-Y⁷/4). The texture is soft and compressible, but the fibres confer rigidity and coarseness to the overall texture.

Surface. The surface is covered in irregularly disposed, sharply pointed conules, 2.0–4.0 mm high, from which primary fibres often protrude.

Skeleton. The skeleton is a reticulum with very irregular mesh and thick, coarse fibres, 250–2000 µm thick. All fibres are strongly laminate and cored with sand and spicule debris. Despite the coring material, a central pith region is clearly evident.

Soft tissue organisation. A lacunar ectosomal region, 200–400 µm deep underlies a thin collagen reinforced superficial region which is 30–50 µm deep. The choanosome is cavernous with large volume devoted to canals. The mesohyl is reduced in extent and very lightly reinforced by collagen, and the choanocyte chambers are 60–120 µm in longest dimension, oval and eurypylous. There is no interstitial detritus present.

REMARKS

The thick, coarse, cored fibres projecting above the surface and the irregular reticulum characterise this species.

ETYMOLOGY

The generic name emphasises the projecting fibres, and the species name an austral distribution.

DISTRIBUTION

Known only from New Caledonia.

Dictyodendrilla Bergquist, 1980

TYPE SPECIES

Dendrilla cavernosa Lendenfeld, 1886, by original designation Bergquist (1980).

DIAGNOSTIC REMARKS

Dictyodendrillidae in which the reticulate fibrous skeleton forms regular rectangular meshes and is composed of pithed, laminated fibres which are free of any coring material. The tissue construction is delicate and cavernous, and the soft tissue is frequently pale, contrasting with the

dark fibres. The sponges are most often lobate, stalked, or spreading with digitate projections.

Dictyodendrilla elegans (Dendy)

(Fig. 21)

MATERIAL EXAMINED

QMG304699, AUZ 16, Stn. 268, Ilot Maitre, 22°20'02S, 166°22'50E, 19 m depth, 13 Oct 1992. Coll. C. Battershill; BMNH 23.10.1.163 Terra Nova St. 134, Spirits Bay, 20–60 m.

REMARKS

A full discussion of the nomenclature of New Zealand and Australian specimens of *Dictyodendrilla* is given by Bergquist 1994 (in press). Several species can be differentiated, most of which require full description or new names. Bergquist (1980) considered *D. elegans* to be a synonym of *D. cavernosa* (Lendenfeld). That decision is revised here and *D. elegans* is reserved for northern New Zealand specimens and the present specimen, which is the first record of the genus from New Caledonia.

DISTRIBUTION

Northern New Zealand, New Caledonia.

Order VERONGIDA Bergquist, 1978

DIAGNOSTIC REMARKS

Ceractinomorpha in which a fibre skeleton is always present, and this may be anastomosing or dendritic in construction. The latter condition is always associated with a reduction in fibre in relation to soft tissue volume. Dendritic skeletons have an overall divergent plan, as the term implies, but there is frequent fasciculation along individual branches caused by divergence and convergence of the complex, irregular fibre elements. Thus, 'dendritic' as applied to verongid skeletons refers to an overall divergent pattern but one which is not implemented rigidly as in the Dendroceratida.

In verongids with anastomosing skeleton the meshes are polygonal, and there is no distinction between primary ascending and secondary connecting elements. Fibres can become organised into a single plane either throughout the sponge or as lamellae near the surface; occasionally intertwined fascicles of fibres emphasise such sur-

previous page

FIG. 20. A–C, *Acanthodendrilla australis* sp. nov. A, Holotype QMG304698, preserved specimen (x 1.5). B, Photomicrograph of fibre in cross section (x 200). C, Photomicrograph of a portion of the fibre skeleton (x 100).

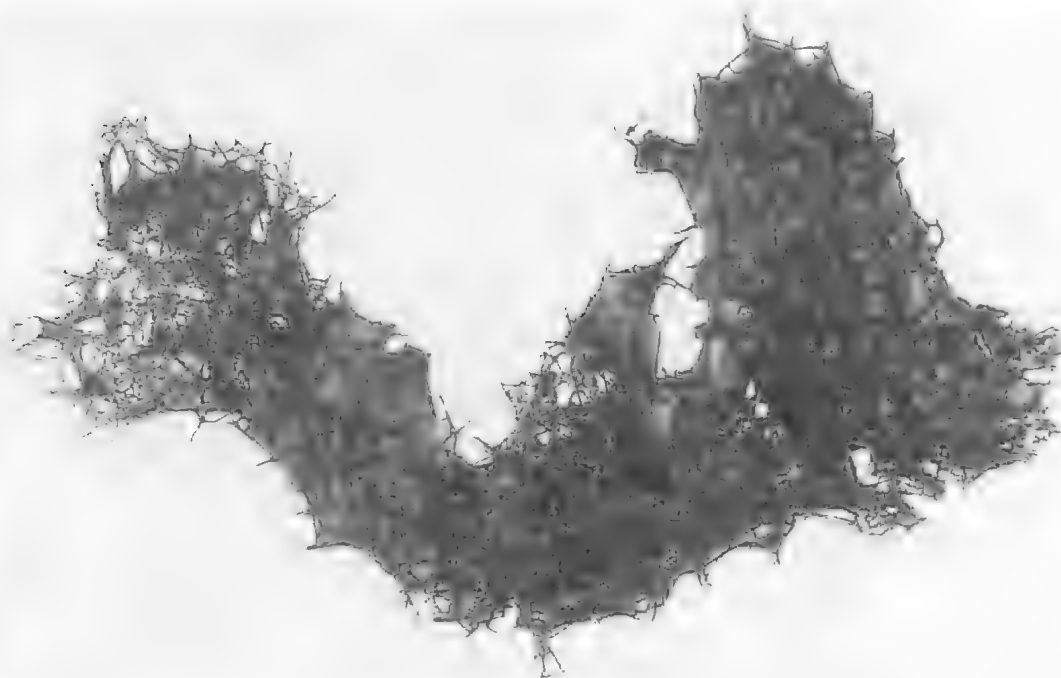


FIG. 21. *Dictyodendrilla elegans* (Dendy) QMG304699, preserved specimen (x 1.0).

face specialisation. The typical fibre structure is a markedly concentric laminar bark surrounding a pith of fine fibrillar material. Both bark and pith elements can be reduced and bark is lost entirely in one genus, but some elements are always present. Fibrous spicules separate from the main skeleton and composed only of bark elements occur in one genus. The boundary between bark and pith is very marked, and the fibres on drying appear hollow. Cellular elements (spongocytes) become incorporated in the fibres in one family. Fibres rarely contain foreign detritus. Choanocyte chambers are diplodal, sac-shaped or slightly tubular, and are set in a matrix in which many different cell types are represented and which is densely infiltrated by fibrillar collagen. A collagenous ectosome is usually differentiated. The texture of verongioid sponges reflects the collagenous nature of the matrix, they are homogeneous, deformable and fleshy. A very common pigmentation is sulphur yellow tinged with green; on death or damage this oxidises rapidly to dark brown, or more frequently deep purple, almost black. The mode of reproduction is oviparous; the structure of the larvae is unknown. Verongida are extremely distinct biochemically. They have no ter-

penes, but a lipid fraction high in sterol within which novel aplystane sterols frequently dominate. A series of tyrosine-derived brominated compounds occur in all genera that have been studied.

Family APLYSINELLIDAE Bergquist, 1980

DIAGNOSTIC REMARKS

Verongida with a dendritic skeletal pattern in which the pith elements of the fibres are emphasised and the bark component can be reduced or absent. The fibre skeleton is sparse in relation to the matrix volume, and it may be augmented by spongin spicules formed of bark elements. The choanocyte chambers are diplodal, small, and spherical; the matrix is strongly collagenous. Pigmentation is frequently sulphur yellow, with the same oxidation characteristics as for the Aplysinidae. However, some species have superficial pink to purple colouration and a beige to pale yellow interior and this pigmentation is stable in alcohol.

Porphyria gen. nov.

TYPE SPECIES

Porphyria flintae sp. nov.

DIAGNOSIS

Aplysinellidae with the typical dendritic skeleton with fibres having short, often flexuous branches and reduced pith component. Fibres are abundant. The sponge is in the form of a goblet and is a rich purple colour externally.

ETYMOLOGY

For the rich purple colour.

Porphyria flintae sp. nov.

(Fig. 22A-D)

MATERIAL EXAMINED

HOLOTYPE: QMG304700 ORSTOM (R193), Stn. 188, Maré, Cap. Boyer, 21°37'08S, 168°06'08E, 30-35m depth, 24 Jun 1977. Coll. P. Laboute.

PARATYPES: ORSTOM (R.340), Stn. 114, Banc Gail (lagoon), 22°22'04S, 166°39'02E, 35-38m depth, 29 Jun 1976. Coll. P. Bourret, ORSTOM (R246), St. 172, Ile des Pins, 22°43'10S, 167°30'04E, 30m depth, 7 Jan 1977. Coll. A. Intés.

DIAGNOSIS

As for genus.

DESCRIPTION

A stalked goblet shaped sponge with distinct internal oscular and external poral faces. The holotype is 7cm high, 7cm across, the wall of the cup is 1.5cm thick at its mid-point, and the stalk is 1.5cm thick. A second specimen is 7cm high, 5.5cm across, 1cm wall thickness, with a stalk 0.5cm thick. Larger specimens up to 20cm high and 15cm wide have been recorded. Oscules are small 1.0mm in diameter, circular, each located in a slight depression on the inner face of the vase and surrounded by a membranous rim. The colour is pale to deep purple ($bP^6/8$ to $bP^7/8$) externally, and cream ($Y^3/4$) internally, in spirit purple black ($rR-P^2/2$). The texture is firm, rubbery but compressible.

Surface. The interior surface of the vase is smooth; the exterior is just roughened by fine low conules and can be smoothly contoured or thrown into mounds.

Skeleton. The skeleton is made up of slender dendritic fibres ramifying from a centre basal point which is either a narrow or broad stalk. For most of their length the main fibres are of even dimension, 60-80µm thick. They taper to sharp

points near the surface, narrowing to 15-30µm diameter. The branch fibres arising from the main dendritic elements are short, typically 30-350µm long, flexuous and often sharply pointed. Pith makes up one quarter to one third of the fibre thickness, the surrounding bark is very dense and tightly laminated. This renders the fibres extremely brittle.

Soft tissue organisation. The ectosome is a well marked region, 110-140µm deep, with an outer layer 20-30µm in extent which contains little collagen and has a high number of spherulous and other secretory cells. The deeper region is strongly collagen reinforced, but also contains many spherulous cells superficially. The choanosome is very evenly collagen reinforced and choanocyte chambers are diplodal, spherical and small, 15-30µm in diameter.

REMARKS

Porphyria is distinct from other genera of the Aplysinellidae, in having abundant branched fibres with reduced pith component. The shape and brilliant purple colour are also distinctive. One sulphur-yellow specimen has been found (ORSTOM R1340). Such variation in pigmentation in all Verongida depends upon the oxidation state of the body pigments and is always observable upon death or damage.

ETYMOLOGY

For Professor Valerie Flint, medieval historian, who has provided help with many sponge names.

DISTRIBUTION

Known only from New Caledonia.

Pseudoceratina Carter, 1885

Psammaphysilla Keller, 1889; *Korotnewia* Polejaceff, 1889; *Druinella* Lendenfeld, 1889.

TYPE SPECIES

Pseudoceratina durissima Carter, 1885, by subsequent designation of de Laubenfels (1948).

DIAGNOSIS

Aplysinellidae with sparse fibre skeleton organised on the dendritic plan typical of the family. Pith elements only are present in the fibres. The matrix of the sponge is extremely dense and heavily reinforced by collagen; the texture is hence firm, and often extremely hard and incompressible. The surface of the sponge is conulose or tuberculate.

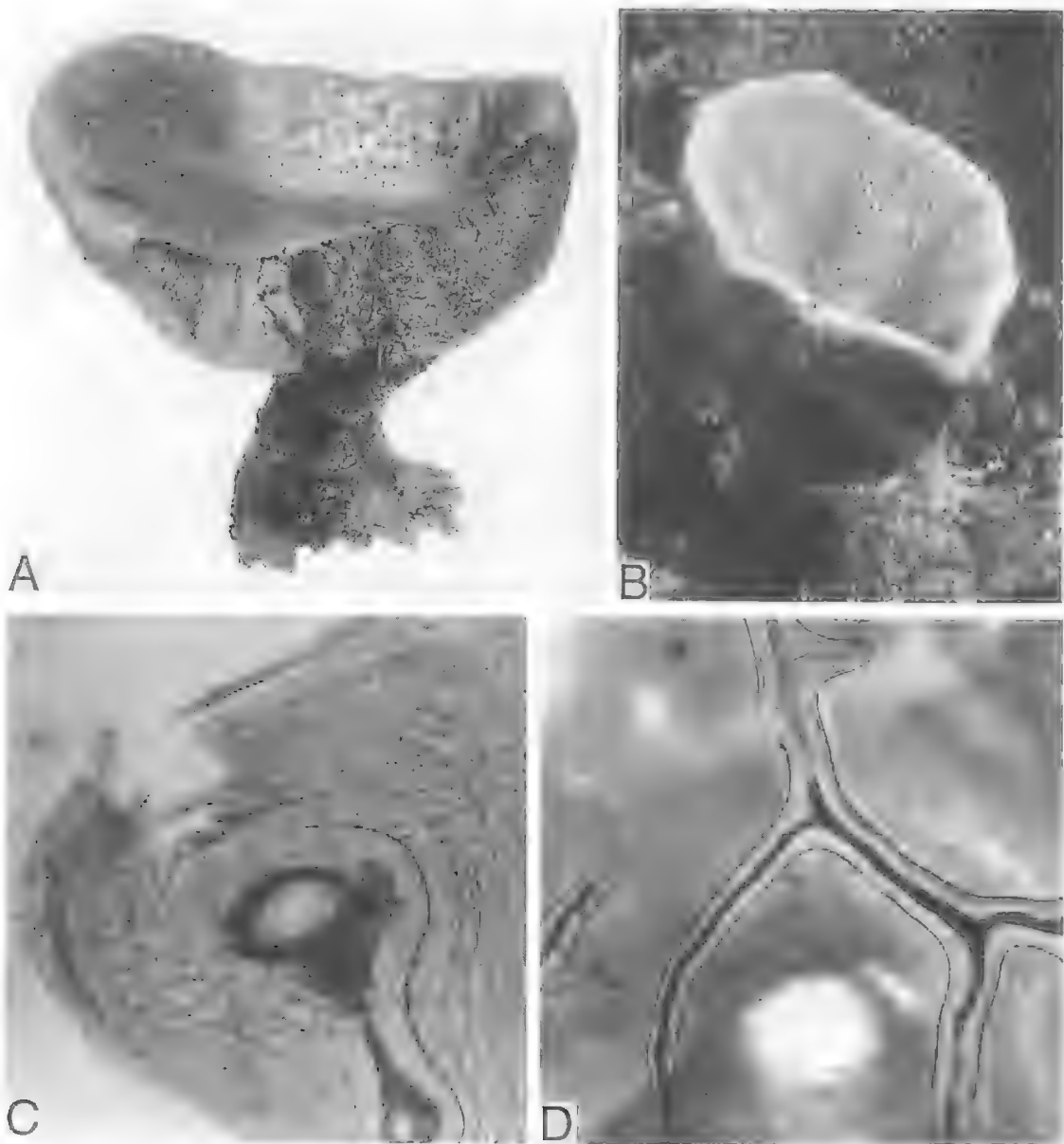


FIG. 22. A-D, *Porphyria flintae* sp. nov. A, Holotype QMG304700, preserved specimen (x 1.0). B, Holotype QMG304700, in situ. (x 0.75). C, Photomicrograph of fibre in cross section (x 300). D, Photomicrograph showing fibre structure (x 80).

REMARKS

Some discussion of the above synonymy is necessary and should be read in conjunction with remarks made later relating to *Suberea*. The type specimen of *Pseudoceratina durissima* Carter is BMNH 83.4.12.48 as indicated by Bergquist (1980). This sponge is in an excellent state of preservation and sections taken from this speci-

men have been re-examined in the course of this work. This specimen has very firm texture as a result of dense collagen aggregations throughout the body; it has sparse fibre content and the fibres lack a bark component; they also contain some sandy material. Slides registered as BMNH 86.12.15.86a are inscribed 'type' also. These are thick sections and have been examined, and in all

features they are identical to those of BMNH 83.4.12.48. An earlier diagnosis of *Pseudoceratina* (Bergquist 1980) was based upon observation of thick sections only and these gave an impression that there were traces of a refractile bark present in the fibres. This is not the case as new histological sections show. The sponge has only pith elements in which scattered, not organised, sandy detritus is incorporated. As a consequence of this, the suggested distinction in fibre structure which sustained recognition of *Psammaphysilla* Keller as distinct from *Pseudoceratina* Carter cannot be made, and the former becomes a junior synonym of the latter.

In the absence of a type specimen, Bergquist (1965, 1980) considered the genus *Druinella* Lendenfeld, based on the type description, to be unrecognisable except as a synonym of *Psammaphysilla*. Wiedenmayer (1989) reported that he had located a type specimen of *Druinella* in Berlin. Following study of this, he confirmed the identity of *Druinella* with *Psammaphysilla* and recognised *Druinella rotunda* Lendenfeld as a good species, distinct from *Psammaphysilla purpurea* (Carter), the type species of *Psammaphysilla*. In taking his analysis further, Wiedenmayer failed to consider the histology and fibre structure of the holotype of *Pseudoceratina durissima*. Consequently, both his elevation of *Druinella* as the senior synonym, and the elevation of the name Druinellidae to displace Aplysiniellidae as the appropriate family name are invalid. Wiedenmayer's work (1989) displays little understanding of the structure and organisation of the 'keratose' sponges, and in many cases he has several different species represented under one name. His discussion of *Pseudoceratina* and *Druinella* provide two examples of such confusion. By his own admission he worked from poor, thick sections. This is simply not adequate for descriptions of Verongida or indeed other 'keratose' sponges. Wiedenmayer's attempt to infer dubious status for the holotype of *Pseudoceratina durissima* can be dismissed, as can the comment to that end by Pulitzer-Finali (1982). Neither author looked at the histology of the type, either specimen or slide; it is entirely consistent with Carter's description; both authors were emphasising as a point of distinction the fact that *Pseudoceratina* was diagnosed by Bergquist (1980) as having both bark and pith elements in the fibres, while Carter had noted only pith elements. The above discussion corrects this misinterpretation.

There are two further points to address. Throughout the tropical Pacific and extending southward to temperate Australian waters, massive Aplysiniellidae with sparse dendritic fibres with both pith and bark elements present, and very dense, often highly regionalised collagen aggregations are common. These specimens have been referred to in the main as *Pseudoceratina*, they now require a new name and *Suberea* is proposed in this paper, and species which can be assigned to it with confidence are named. In South Eastern Australia and in New Caledonia specimens of *Pseudoceratina* and *Suberea* are found commonly in the same habitats. They are similar in pigmentation, in their range of growth forms and surface organisation. All turn dark purple and become extremely hard in spirit or in a dry state. It is understandable that confusion has arisen; the major distinctions are in fibre structure and soft tissue organisation, but these distinctions are clear.

Bergquist et al. (1991) reintroduced the Druinellidae as a family separate from the Aplysiniellidae and recorded a specimen from New Zealand as being a second species of *Druinella*. The separation of the two families was based upon a very divergent sterol composition in the New Zealand specimen and its unique fibre structure. The fibres are dendritic and very thin, with both bark and pith elements present but the latter is extremely reduced. The fibres are extremely irregular, thrown into curves and with complex knotted outgrowths of the bark some of which appear to be free spongin rods or spheres. Only one specimen of this sponge has been found. It is very distinct from the Australian *Druinella* records now correctly referred to as *Pseudoceratina rotunda* and will require a new family to be established for its reception. That will be done in a forthcoming monograph on the New Zealand Sponge Fauna. In the meantime further specimens are being sought. The status of the genus *Aiolochoia* Wiedenmayer will be considered under the discussion of *Suberea*.

Pseudoceratina verrucosa sp. nov.
(Fig. 23A-C)

MATERIAL EXAMINED

HOLOTYPE: QMG 304701 ORSTOM (R191), Stn. 186, 110t Vauvilliers, Lifou, 21°07'09S, 167°34'00E, 10-35m depth, 21 Jun 1977. Coll. P. Laboute.
PARATYPE: ORSTOM (R1327), Beutemps Beaupre, 40m depth, 23 Nov 1981. Coll. P. Laboute. (Bergquist, personal collection, no co-ordinates or Station number). ORSTOM (R570), Stn. 113, Grand récif M'Bère,

22°21'01S, 166°14'00E, 25-35m depth, 21 Jun 1976.
Coll. P. Laboute.

DIAGNOSIS

Pseudoceratina having a strongly verrucose surface, a sparse skeleton and thick coarse fibres.

DESCRIPTION

A massive, repent sponge with thick branches spreading over coral substrate; individuals can cover areas up to 30cm across. The holotype is 12cm long, 4cm wide and 3.5cm thick with irregular contours. Oscules are prominent, 2-3mm in diameter scattered over the upper surface, slightly elevated with a pronounced contractile rim. The colour throughout is dull yellow (rY⁷/6) to brown yellow (rY⁶/8) in life, in spirit purple black (rR-P²/2). The texture is hard and incompressible.

Surface. The surface is characterised by abundant conules 1-2mm high, which are rounded rather than pointed apically. The general body surface is uneven with low ridges present in places.

Skeleton. The skeleton is dendritic, made up of irregular fibres which are composed only of pith elements and which always enclose a small amount of sandy debris. The surface of the fibres resembles a solidified lava flow. Large areas of the body are devoid of skeleton; this is particularly so in the deeper region of the choanosome. The irregularity of the fibres makes measurements rather meaningless, but the range is from 220-600µm in diameter.

Soft tissue organisation. This sponge has strong collagen tracts deployed regionally to structure both the ectosome and the choanosome. All canals are surrounded by dense collagen depositions. In addition, collagen tracts surround fibres and divide the choanosome into islands of tissue in which the choanocyte chambers, 15-20mm in diameter lie. The ectosome is strongly collagenous, 300-800µm deep, made up of alternating bands of extremely dense collagen separated by areas which have a lower collagen content and high concentrations of spherulous cells. There are large canal lacunae along the inner boundary of the ectosome and in the immediate subsurface region there is a regular array of small inhalant canals.

REMARKS

The features which distinguish *P. verrucosa* from *P. purpurea* (Carter), the other common tropical species of the genus, are the strongly verrucose surface of the former as opposed to the predominance of sharp conules in the latter. Also, *P. purpurea* has abundant relatively fine fibre elements distributed evenly throughout the sponge, while *P. verrucosa* has a sparse skeleton and thick coarse fibres. Sandy inclusions in the fibres are rare in *P. purpurea* but consistently present in *P. verrucosa*.

Other species which now can be assigned to *Pseudoceratina* are *P. arabica* (Keller), which could prove to be conspecific with *P. purpurea*, and *P. durissima* Carter which almost certainly should receive Lendenfeld's sponge described as *Druinella rotunda* as well as the specimen allocated to that species by Wiedenmayer (1989). It will be necessary to refer to Lendenfeld's type specimen before confirming that synonymy. Further species of *Pseudoceratina* remain to be described from Australia.

ETYMOLOGY

The species name refers to the rough verrucose surface.

DISTRIBUTION

Known only from New Caledonia.

Suberea gen. nov.

TYPE SPECIES

Suberea creba sp. nov.

DIAGNOSIS

Aplysinellidae with coarse irregular dendritic fibres in which bark and pith elements are present but the pith predominates. The bark is strongly laminated and very brittle. Fibres can be very thick and render the texture of the sponge interior very rough. Dense collagen reinforces the matrix, rendering the sponges hard to just compressible. The surface is smooth or conulose and the sponge form massive, sometimes stalked or branching.

REMARKS

Species which fall into this genus are predominantly those which have been referred to

overleaf

FIG. 23. A-C, *Pseudoceratina verrucosa* sp. nov. A, Holotype QMG 304701, in situ (x 0.75) B,C, Photomicrographs of the fibre skeleton (x 100).

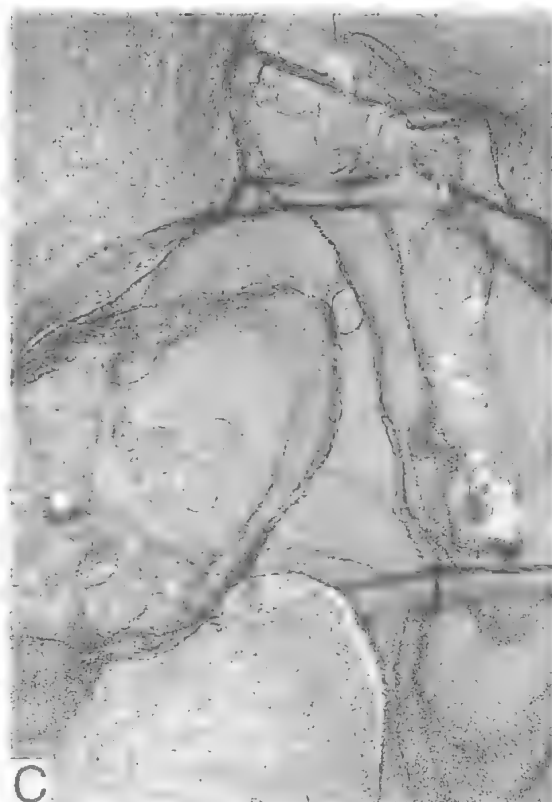
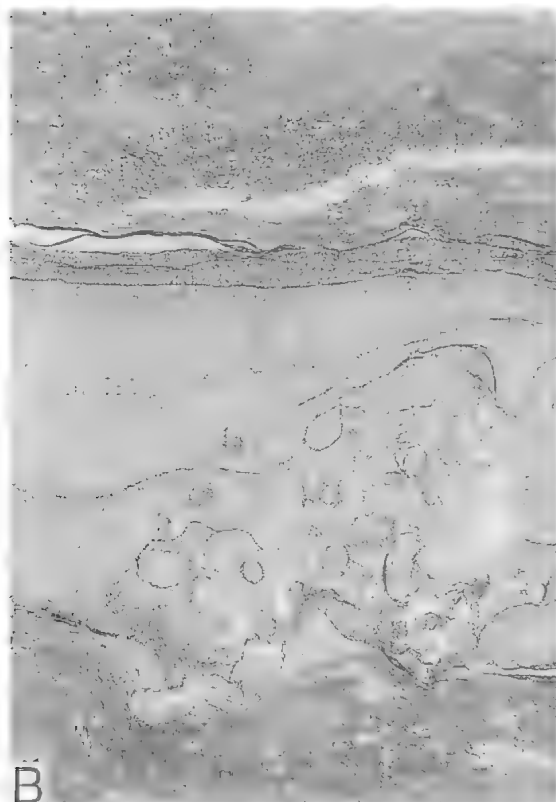
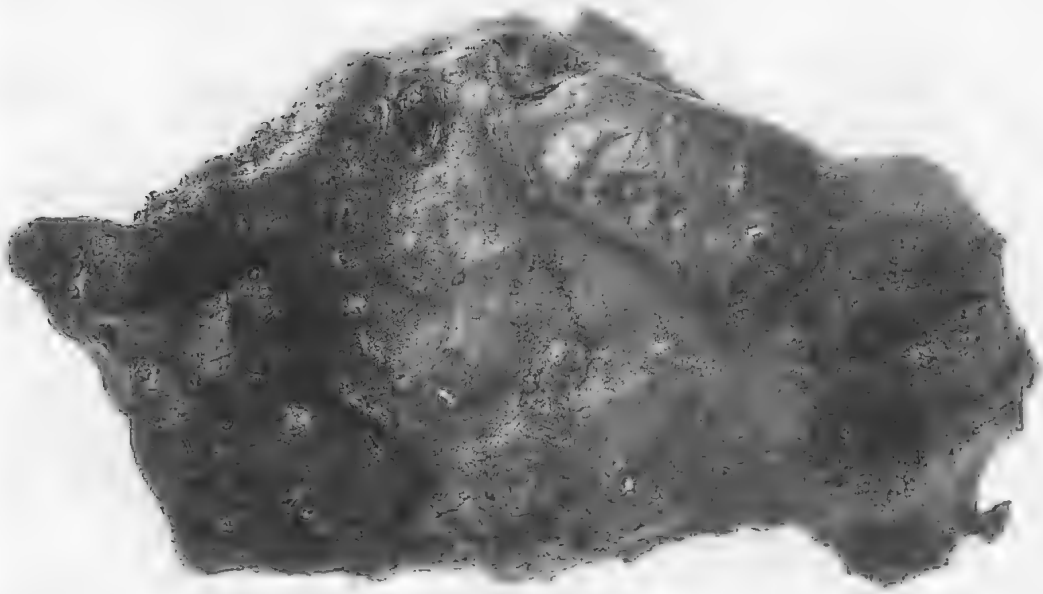


Fig. 23



A



B

Fig. 24

Pseudoceratina subsequent to Carter (1885) and following the diagnosis of that genus by Bergquist (1980) which stated that bark components were present in the fibres. As indicated earlier, confirmed by examination of the type specimen of *Pseudoceratina*, that genus lacks bark investing the fibres. A new name is consequently required for the present species group in which both bark and pith elements are present. There are a number of species from Tropical eastern and west Australia which need to be described under this name. *Pseudoceratina clavata* Pulitzer-Finali (1982) is the only described species which can be referred, although it is clear from his illustrations, that Wiedenmayer (1989: pl.37, figs 5,6) had lumped species with this fibre structure in with those referable to *Pseudoceratina* based on the characteristics of the type species.

The position of *Pseudoceratina crassa* (Hyatt) from the Caribbean needs clarification. It should be separate at the generic level from *Suberea*. It does not have the coarse fibre structure and the strong collagen reinforced matrix of that genus and the pitted contoured surface and pigmentation serve to further distinguish it. The name *Aiolochoira* Wiedenmayer, with synonym *Dendrospongia* Hyatt, should be reserved for this species.

ETYMOLOGY

The generic name refers to the corky texture of these sponges and translates as 'like cork'.

Suberea creba sp. nov. (Fig. 24A, B)

MATERIAL EXAMINED

HOLOTYPE: QMG304702, ORSTOM (R1280), Stn. 151, Passe de St Vincent, 22°03'04S, 165°58'03E, 45m depth, 10 Sep 1976. Coll. P. Laboute.

DIAGNOSIS

Suberea with spreading habit, smooth surface and dense texture.

DESCRIPTION

A massive spreading sponge of irregular shape, covering an area 10cm by 15cm, to a thickness of

3-4cm. Oscules are 2-3mm in diameter, scattered, slightly elevated, and surrounded by a contractile collagenous rim. The colour in life is bright yellow ($Y^6/10$), in spirit purple black (rR-P²/2), and the texture hard and cork like.

Surface. The general surface is smooth but the body is thrown into lumps and folds, giving a tuberculate impression.

Skeleton. The skeleton is dendritic, sparse and made up of fibres which are usually circular in cross section and composed of both bark and pith elements, the latter accounting for about three quarters of the diameter. The lamination of the bark fibre elements is not very evident but concentric fracture planes appear in sections. Typical fibre dimensions are 120-250µm in diameter.

Soft tissue organisation. A strongly collagenous ectosome 500-600µm deep is sharply separated from an underlying choanosome which is evenly collagen reinforced throughout. Spherulous cells are concentrated in the ectosome and along canals throughout the body. The external boundary of the ectosome is a fibre cuticle, 5-8µm deep; it is probable that this is transient but comparable structures have been reported in other Verongida (Bergquist, 1980). Choanocyte chambers are spherical, 15-20µm in diameter.

REMARKS

The spreading habit, smooth surface and fibre structure separate *S. creba* from the only other described species, *S. clavata* (Pulitzer-Finali 1982).

ETYMOLOGY

The species name refers to the dense texture of the sponge.

DISTRIBUTION

Known only from New Caledonia.

Suberea laboutei sp. nov. (Fig. 25A-C)

MATERIAL EXAMINED

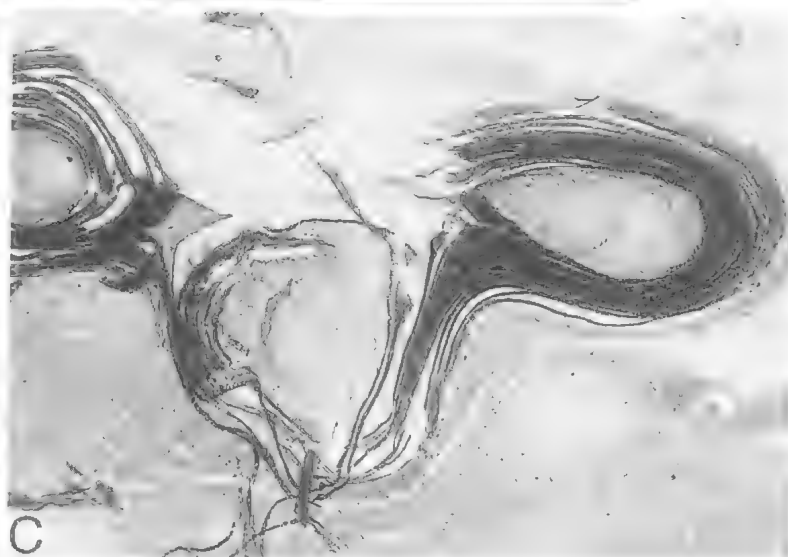
HOLOTYPE: QMG304703 ORSTOM (R1309), Stn. 320, Lagon nord, 19°02'50S, 163°33'30E, 18m depth, 21 Aug 1981. Coll. P. Laboute.

previous page

FIG. 24. A-B, *Suberea creba* sp. nov. A, Holotype QMG304702, preserved specimen (x 1.5). B, Photomicrograph of fibre in cross section (x 100).

facing page

FIG. 25. A-C, *Suberea laboutei* sp. nov. A, Holotype QMG 304703, in situ (x 1.0). B,C, Photomicrographs of fibre in cross section (x 100).



DIAGNOSIS

Suberea of multilobate form, having pronounced conulose surface and a strongly laminated brittle fibre structure.

DESCRIPTION

An erect, lobate sponge, 7cm high, 8cm wide, 4cm thick, loosely adherent to the coral substrate at multiple attachment points. Oscules are prominent, circular, 3-7mm in diameter, situated toward the apex of individual lobes and surrounded by a thickened membrane. The colour in life is dull yellow (Y-R-Y⁷/10), in spirit chocolate brown (Y-R-Y³/4). The texture is firm, but compressible.

Surface. The surface is covered in pointed conules, 1-3mm high which tend to be aligned into short rows, giving the surface a ridged appearance. The surface contour is very irregular, with many thin projections from the main lobes of the body.

Skeleton. The skeleton is dendritic and fibres are relatively abundant. They are spherical to oval in cross section. Sometimes two or three adjacent fibres are incorporated within common bark laminae. Both bark and pith elements are present. The bark has strongly defined, thin, concentric laminae which separate and fragment when sectioned. It never makes up more than one quarter of the fibre diameter and can be reduced to one tenth. Pith is the dominant element in all fibres. Fibres range from 200 to 700µm in maximum dimension.

Soft tissue organisation. There is a distinct ectosomal region 250-350µm deep, marked by islands of dense collagen deposition between which lie tracts of cells, most of which are spherulous cells. These make up an almost continuous surface layer. The choanosome is evenly collagen reinforced except around major canals, where collagen is heavily emphasised. Choanocyte chambers are spherical, 10-15µm in diameter.

REMARKS

The pronounced conulose surface, multiple lobate form, and the strongly laminated, brittle fibre structure distinguish *S. laboutei* from other species of the genus.

ETYMOLOGY

The sponge is named after M. Pierre Laboute, ORSTOM, who collected and photographed many of the specimens described in this work.

DISTRIBUTION

Known only from New Caledonia.

Family LANTHELLIDAE Hyatt, 1875

DIAGNOSIS

Verongida in which the fibre skeleton is anastomosing, frequently compressed into two dimensions, and radiating from a contracted base of attachment. Fibres contain cellular elements in distinctive concentric annuli; these occur mainly in bark elements, but are in pith as well. The fibres are of typical construction for the order. Individual fibres can attain great thickness, particularly towards the base of the sponge. The choanocyte chambers are large, and sac-shaped (*lanthella*) to slightly elongate and occasionally branched (*Anomoianthella*). Where colour in life is known, it ranges from typical verongid sulphur yellow through deep orange to deep purple. All species show the characteristic oxidation reaction upon damage or death, and reach a final deep purple colouration. Biochemical characteristics are similar to those of the Aplysiniidae and Aplysiniellidae with respect to the occurrence of brominated metabolites. Thus far, no aplystane sterols are known from any species of lanthellidae; these characterise the Aplysiniidae and Aplysiniellidae, which are almost identical in their major biochemical characteristics.

REMARKS

Previous diagnoses of the family Lanthellidae have included reference to *Bajalus* Lendenfeld, a problematic sponge which lacks a fibre skeleton, has sac shaped to slightly branched choanocyte chambers and a distinct collagenous ectosome. Bergquist (1980) referred *Bajalus* to the lanthellidae, noting coincidence of choanocyte chamber structure and ectosomal development between *Anomoianthella* and *Bajalus*. More recently, species of *Halisarca* with highly organised ectosomal regions have been described (Vacelet and Donadey, 1987) and fresh material of Lendenfeld's sponge has been discovered from the Southern New South Wales coast where it is common growing on *Pyura*. Examination of this material confirms that it is a *Halisarca* properly referred to as *H. laxis*. Consequently, reference to Lanthellidae and Verongida as including forms which lack a fibrous skeleton has been deleted from the diagnoses.

***Ianthella* Gray, 1869**

Basta Oken, 1815; *Haddonella* Sollas, 1903.

TYPE SPECIES

Ianthella flabelliformis Pallas, 1776, by subsequent designation of Topsent (1905).

DIAGNOSTIC REMARKS

Ianthellidae in which the fibrous skeleton is highly developed and makes up by far the great bulk of the sponge body. The skeleton is a reticulate structure typically developed in a single plane to produce a regular fan shape. Elaborations of the simple two-dimensional fibre arrangement which characterises *I. basta* are in the form of two-dimensional extensions almost at right angles to the basic reticulum as for example, in *I. flabelliformis*. Fibres are of typical construction, with both bark and pith elements represented. The bark contains many spongocytes arranged in concentric annuli.

***Ianthella basta* (Pallas)**

Spongia basta, Pallas, 1766: 309.

Ianthella basta, Gray, 1869: 51; Bergquist, 1980: 498.

MATERIAL EXAMINED

ORSTOM (R401), Stn. 114, Banc Gail, 22°22'04S, 166°39'02E, 35-38m depth, 29 Jun 1976. Coll. P. Bourret. *Spongia striata* Lamarck DT523 No 48, Natural History Museum, Paris.

REMARKS

Ianthella basta is the best known and most easily recognised species of *Ianthella*. This is in part due to its wide distribution in the Indo-West Pacific, and thus its presence in older collections, but it is mainly due to the morphology of the sponge. The thin, two dimensional fan or vase-like form of *Ianthella basta* is very distinctive, and the fine reticulation of fibres in highly regular rectangular meshes, is very striking. *Ianthella basta* has been well illustrated and described by Lendenfeld (1889) and Topsent (1931, as *Spongia striata* Lamarck). In all specimens examined, there is no development of extensions of the basic two-dimensional fibre skeleton. *Ianthella basta* is also remarkable in that it exhibits the full known range of verongid colouration in a single species. There are no differences in fibre construction and arrangement or chemistry between specimens with differing colouration. De Laubenfels (1948) referred *Spongia striata* Lamarck to *Ianthella flabelliformis*; *Spongia*

striata has been examined and it is definitely a specimen of *I. basta* Pallas, having the fine regular rectangular network characteristic of the species.

DISTRIBUTION

Northern Australia, Torres Straits, Papua New Guinea, Guam, Mascarene Islands, Indian Ocean, New Caledonia.

Anomoianthella* Bergquist, 1980*TYPE SPECIES**

Anomoianthella popeae by monotypy, Bergquist (1980).

DIAGNOSTIC REMARKS

Ianthellidae with thickened fan-shaped, club-shaped, or cup-shaped growth form, always having a discrete oscular and poral surface or a localised oscular region. The construction of the sponge is cavernous, with extremely thick fibres which form an irregular anastomosing reticulum; soft tissue is sparse in relation to fibrous material. The fibres are of typical construction, with substantial pith and a bark component in which numerous spongocytes are arranged in concentric annuli. There is no compression of the skeleton into a single plane as in *Ianthella*. The choanocyte chambers are eurypylous, but are elongate-oval and sometimes branched in a manner which recalls the chamber construction of *Halisarca*.

***Anomoianthella rubra* sp. nov.
(Fig. 26A-D)****MATERIAL EXAMINED**

HOLOTYPE: QMG304704, Stn. 268, Ilot Maitre, 22°20'02S, 166°22'50E, 19m depth, 13 Oct 1992. Coll. J. Vacelet (no ORSTOM number).

PARATYPES: ORSTOM (R875), Stn. 183, Passe de Kouaré, 22°47'05S, 166°44'06E, 25m depth, 7 Jun 1977. Coll. P. Laboute. QMG304705, ORSTOM (R171), Stn. 136, Ilot Canard, 22°19'02S, 166°21'07E, 12-20m depth, 16 Apr 1981. Coll. P. Laboute.

DIAGNOSIS

Anomoianthella with less developed ectostome with patchy cuticle, fine fibres, large choanocyte chambers and a brilliant orange-red colour in life.

DESCRIPTION

The holotype is a cavernous spreading fan, rising from a base 2cm in diameter to a height of 15cm and width of 13cm. The body is up to 3.0cm thick. Another specimen from the same collection

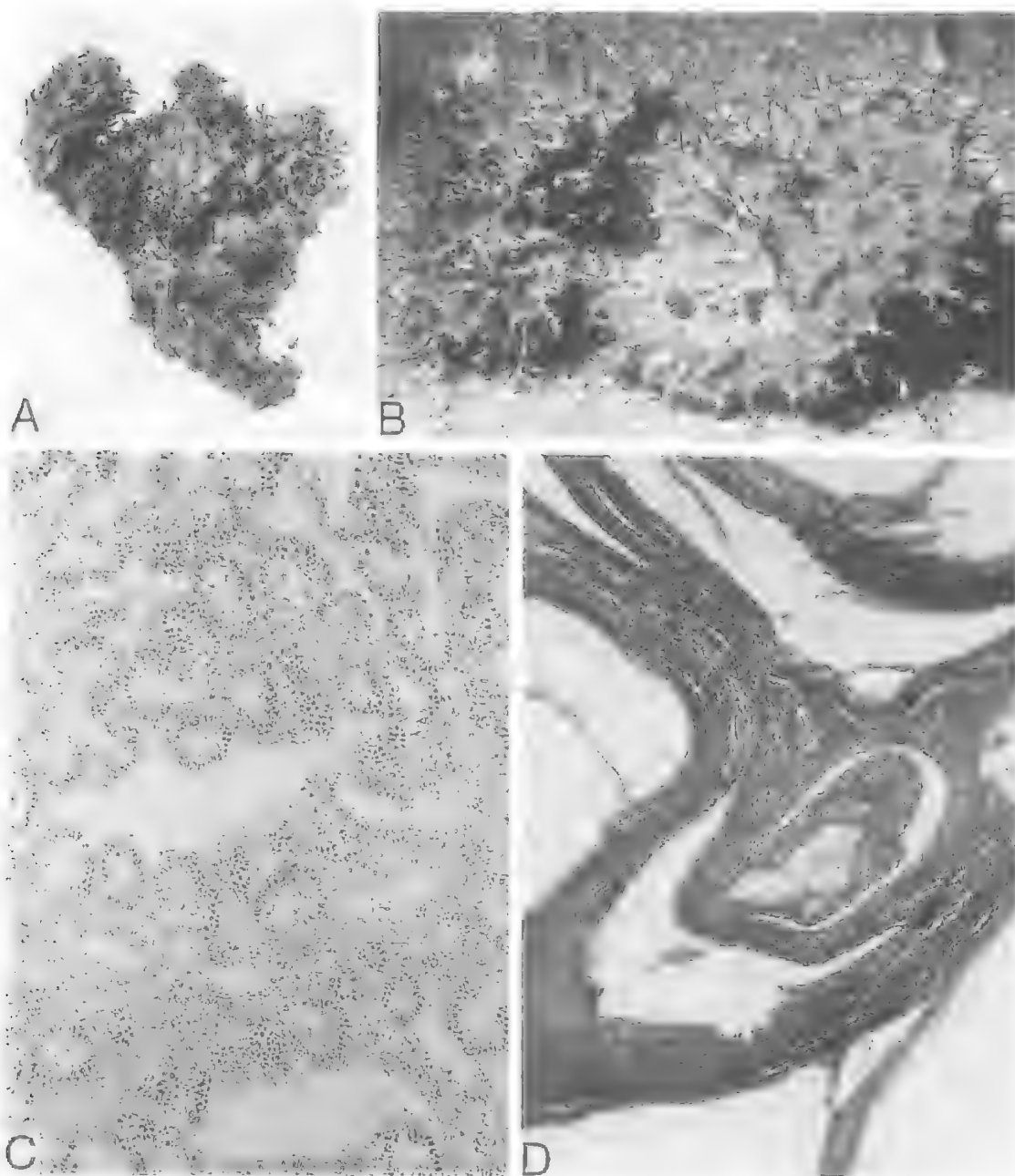


FIG. 26. A-D, *Anomoianthella rubra* sp. nov. A, Holotype QMG304704, preserved specimen (x 0.2). B, QMG304705(R171), in situ (x 0.5). C, Photomicrograph of choanosome (x 400). D, Photomicrograph of fibre in cross section (x 100).

is a more compact, low, fan 5cm high, 8cm wide, 4cm thick, with a broad attachment base. Oscules are large, irregular in shape, up to 1.2cm in maximum dimension, scattered over the whole body but they are most common along the apex of the fan. The flesh colour in life is brilliant orange-red

(y-R⁶/12), the contrasting fibres dark red (R³/8); in spirit the sponge is uniformly purple black (rR-P²/2). The texture is compressible, rendered rough by the dominance of fibres.

Surface. The surface is covered in coarse, sharply pointed conules up to 6mm high and

supported by single or branched fibres, many of which run a considerable distance in the plane of the surface.

Skeleton. The skeleton is made up of extremely thick fibres diverging from the base but anastomosing to form a very irregular, open reticulum. Individual fibres are slightly flattened, oval in cross-section, and up to 2500µm in maximum sectional dimension. Fibres contain both bark and pith elements, the latter making up approximately one third of the diameter in each. The bark is strongly laminated and charged with cellular elements, which are arrayed in annuli which fracture apart into strings of fibre and cells on sectioning. The bark grades into the pith, there is no clear boundary between the two regions, and cellular elements are present throughout the pith but are not in a concentric arrangement.

Soft tissue organisation. A narrow collagen reinforced ectosome is present, 120-200µm deep, marked by concentration of spherulous cells and set off from the cavernous choanosome by subdermal lacunae. In places a cuticle 20µm thick covers the surface. It is made up of fibre and encloses cells in exactly the same arrangement as in the fibres. The choanosome is lightly collagen reinforced, largely made up of canals and choanocyte chambers which are eurypylous, chiefly oval, but in some cases slightly branching, 70-110µm in longest dimension.

REMARKS

Anomoianthella rubra is distinct from the only other described species of the genus, *A. popeae* from Western Australia, in having a less developed ectosome with patchy cuticle, slightly finer fibres, larger choanocyte chambers, and in its colour.

ETYMOLOGY

The species name refers to the orange red colour.

DISTRIBUTION

Known only from New Caledonia.

CONCLUSION

Previous authors, based on largely on deep water collections, suggested that the levels of endemism in the New Caledonian sponge fauna are relatively high, at around 60% for the group as a whole (Lévi 1967, Lévi & Lévi 1983a,b). Lévi (1979) observed that the shallower water fauna contained far fewer endemic species, and

had a significant widespread Indo-Pacific element. Two contributions in the present series of papers (Hooper & Lévi 1993a, 1993b), dealing with the orders Poecilosclerida and Axinellida respectively, come to rather different conclusions, recording 63% endemism for shallow water reef Poecilosclerida and 48% endemism for Axinellida, inclusive of the deep water component with no notable Indo-Pacific element being identified.

So many species remain undescribed throughout the southern oceans, that deriving percentage figures for endemism has little meaning. Also, the standard of the published literature is so heterogeneous that reference must always be made to deposited specimens; this is a slow process. Intensive studies of individual genera arguably can provide the best indicators, but there are very few available at present.

With the three sponge orders considered here, general problems already stated are compounded by the tendency of authors to lump many species, confusing later workers, and by the fact that many genera superficially appear very similar. To reveal the significant differences requires careful study.

Consequently, no conclusions are offered here on the affinities of the fauna, except to say that there is an Indo-Pacific element recognisable at specific and particularly generic level, and that North Eastern and West Australian affinities also emerge. New Zealand and Temperate Australian affinities depend upon one species only. The high number of endemic species is almost certainly a function of lack of collections and/or faulty identifications in adjacent regions.

ACKNOWLEDGEMENTS

I am extremely grateful to Dr Cécile Debitus, ORSTOM, Noumea, for assisting with the acquisition of specimens and data, which has greatly facilitated the preparation of this publication. I also gratefully acknowledge funding provided by ORSTOM Noumea, DITAC Canberra, and The University of Auckland Research Committee, which enabled the author to participate in a series of workshops at ORSTOM Noumea on the taxonomy of New Caledonian shallow-water sponges. This publication is one of several recent contributions on the shallow-water fauna of the Noumea lagoon, as a prelude to the publication of a popular book on the subject, and I acknowledge the assistance and interaction of my colleagues Chris Battershill, Jane Fromont, John

Hooper, Michelle Kelly-Borges, Claude Lévi, Jean Vacelet and Clive Wilkinson. For collection of specimens and photographs I thank Pierre Laboute, Georges Bargibant, Jean-Louis Menou, and other members of ORSTOM, Noumea for their hospitality, helpful assistance and co-operation during this project. The assistance of Ms Raewyn Eagar, Ms Beryl Davy and Mr Iain MacDonald with microscopy, histology, and photography respectively is acknowledged. Mr S. DeC. Cook provided assistance in the field and laboratory.

LITERATURE CITED

- BERGQUIST, P.R. 1965. The sponges of Micronesia, Part 1. The Palau Archipelago. *Pacific Science* 19 (2): 123-204.
1978. 'Sponges' 1-268. (Hutchinson: London).
1980. A revision of the supraspecific classification of the orders Dictyoceratida, Dendroceratida and Verongida (Class Demospongiae). *New Zealand Journal of Zoology* 7: 443-503.
- IN PRESS. The Marine Fauna of New Zealand, Porifera, Demospongiae Part 5 (Dendroceratida and Verongida). New Zealand, Oceanographic Institute Memoir.
- BERGQUIST, P.R. & WELLS, R.W. 1983. 'Sponge Chemotaxonomy, the development and current status of the field'. Pp.1-50. In P. Scheuer (ed.), *Marine Natural Products* Pt. 5. (Academic Press: New York).
- BERGQUIST, P.R., WILKINSON, C.W. & AYLING, A. 1988. Foliose Dictyoceratida of the Australian Great Barrier Reef. I. Taxonomy and phylogeny. *Marine Ecology* 9 (4): 291-319.
- BERGQUIST, P.R., CAMBIE, R.C. & KERNAN, M.R. 1990a. Sclerane Sesterterpenes from *Collospongia auris*, a New Thorectid Sponge. *Biochemical Systematics and Ecology*. 18: 349-357.
- BERGQUIST, P.R., KARUSO, P. & CAMBIE, R.C. 1990b. Taxonomic Relationships within the Dendroceratida: A Biological and Chemotaxonomic Appraisal. Pp. 72-78. In Rutzler, K. (ed), *New Perspectives in Sponge Biology*. (K. Rutzler, ed.) (Smithsonian Institution Press: Washington).
- BERGQUIST, P.R., KARUSO, P., CAMBIE, R.C. & SMITH, D.J. 1991. Sterol Composition and Classification of the Porifera. *Biochemical Systematics and Ecology* Vol. 19 (1): 17-24.
- BOWERBANK, J.S. 1862. On the anatomy and physiology of the Spongiadae. *Philosophical Transactions of the Royal Society of London* cliii: 747-829, 1087-1135.
- BURTON, M. 1934. Sponges, Pp. 513-621. In 'Scientific Reports of the Great Barrier Reef Expedition 1928-29'. Vol. 4(14), pls 1-2. (British Museum (Natural History): London).
- CARTER, H.J. 1885. Descriptions of sponges from the neighbourhood of Port Phillip Heads, South Australia. *Annals and Magazine of Natural History* (5) 15: 107-117, 196-222, 301-321, pl.4. 16: 277-294, 347-368.
- GRAY, J.E. 1867. Notes on the arrangement of sponges, with description of some new genera. *Proceedings of the Zoological Society of London* (1867): 492-558, pls. 27-28.
- HOOPER, J.N.A. & LÉVI, C. 1993a. Poecilosclerida (Porifera: Demospongiae) from the New Caledonia Lagoon. *Invertebrate Taxonomy* 7: 1221-1302.
- 1993b. Axinellida (Porifera: Demospongiae) from the New Caledonia Lagoon. *Invertebrate Taxonomy* 7: 1395-1472.
- HOOPER, J.N.A. & WIEDENMAYER, F. 1994. Porifera. In Wells, A. (ed) 'Zoological Catalogue of Australia'. Vol. 12. Melbourne: CSIRO Australia. xiii, 626 pp.
- LAL, A.R., CAMBIE, R.C., RICKARD, C.E.F. & BERGQUIST, P.R. 1994. Sesterterpene lacones from a sponge species of the genus *Dactylospongia*. *Tetrahedron Letters* 35 (16): 2603-2606.
- LAUBENFELS, M.W. de. 1936. A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Institute of Washington Publication Number 467. Papers of the Tortugas Laboratory* 30: 1-225, pls 1-22.
1948. The order Keratosa of the phylum Porifera. A monographic study. *Occasional Papers of the Allan Hancock Foundation* No. 3: 1-217.
1954. The sponges of the West-Central Pacific. *Oregon State Monographs, Zoology* 7: 1-306, pls 1-12.
- LENDENFELD, R. VON. 1885. A monograph of the Australian sponges. Part 6. *Proceedings of the Linnean Society of New South Wales* 10: 481-553.
1888. *Descriptive Catalogue of the Sponges in the Australian Museum, Sydney*. (Taylor & Francis: London).
1889. *A Monograph of the Horny Sponges*. (Royal Society: London).
- LÉVI, C. 1967. Démosponges récoltées en Nouvelle-Calédonie par la Mission Singer-Polignac. *Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie. Editions de la Fondation Singer-Polignac* 2: 13-26, pls 1-3.
1979. The demosponge fauna from the New Caledonian area. In 'Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere'. New Zealand Oceanographic Institute Special Volume 1979: 307-315.
1991. Lithistid sponges from the Norfolk Rise, Recent and Mesozoic genera. Pp.72-82. In J. Reitner and H. Keupp (eds.), *Fossil and Recent Sponges*. (Springer-Verlag: Berlin, Heidelberg).

- LÉVI, C. & LÉVI, P. 1983a. Eponges Tétractinellides et Lithistides bathyales de Nouvelle-Calédonie. Bulletin du Muséum National d'Histoire Naturelle (4e série) 5 (A, No.1), 101-168, pls 1-13.
- 1983b. Démospouges bathyales récoltées par le N/O 'Vauban' au sud de la Nouvelle-Calédonie. Bulletin du Muséum National d'Histoire Naturelle (4e série) 5 (A, No.4): 931-997.
1988. Nouveaux spongiaires Lithistides bathyaux à affinités crétacées de la Nouvelle-Calédonie. Bulletin du Muséum National d'Histoire Naturelle (4e série) 10 (A, No.2): 241-263.
- MUNSELL, A. 1942. Book of Color. (Munsell Color Co.; Baltimore).
- POINER, A. & TAYLOR, W.C. 1990. The constituents of Marine Sponges. IV. The isolation of degraded Spongian Diterpenoids from *Aplysilla tango* (sp.nov.) (Dendroceratida). Australian Journal of Chemistry, 43: 1713-1727.
- PRONZATO, R. 1975. Note tassonomiche sul genere *Darwinella* (Porifera). Bulletino d' Museo Istituto di Zoologia dell' Università di Genova 43: 5-20.
- PULITZER-FINALI, G. 1982. Some new or little-known sponges from the Great Barrier Reef of Australia. Bolletino dei Musei e degli Istituti Biologici dell' Università di Genova 48-49 (1980-1981): 87-141.
- PULITZER-FINALI, G. & PRONZATO, R. 1980. The Keratosa in a collection of Mediterranean sponges mainly from the Italian Coasts. Annale del Museo Divico di Storia Naturale di Genova 84: 445-621.
- ROW, R.W.H. 1911. Reports on the marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S. XIX. Report on the sponges collected by Mr Cyril Crossland in 1904-5. Part II. Non-Calcareous. Journal of the Linnean Society, Zoology 31(208): 287-400, pls 35-41.
- SCHULTZE, M.J. 1865. Über ein exemplar von *Hyalonema sieboldi* aus Japan und einem Schwamm mit Nadelnaus Hornsubstanz. Verhandlungen des naturhistorischen Vereins Preussen, Rheinland und Westphalens 22(3):6-7
- SOEST, R.W.M. VAN 1978. Marine sponges from Curaçao and other Caribbean localities. Part I. Keratosa. P.W. Hummelinck & L.J. van der Steen (eds), Studies on the Fauna of Curaçao and other Caribbean Islands, No. 56.
- THIELE, J. 1899. Studien über pazifischen Spongien, II. Zoologica 24: 1-33.
- TOPSENT, E. 1905. Etude sur les Dendroceratina. Archives de Zoologie Experimentale et Générale 4(3), Notes et Revue 8: clxxi-cxcii.
1930. Eponges de Lamarck conservées au Muséum de Paris. Archives du Muséum Nationale d'Histoire Naturelle 6(5): 1-56.
1931. Eponges de Lamarck conservées au Muséum de Paris. Deuxième partie. Archives du Muséum Nationale d'Histoire Naturelle 6(8): 61-124.
- VACELET, J. & DONADEY, C. 1987. A new Species of *Halisarca* (Porifera, Demospongiae) from the Caribbean with remarks on the cytology and affinities of the genus. Pp. 5-12 in Jones, W.C. (Ed.). European contribution to the taxonomy of sponges. (Sherkin Island Marine Station Publications).
- WIEDENMAYER, F. 1889. Demospongiae (Porifera) from northern Bass Strait, southern Australia. Memoirs of the Museum of Victoria 50(1): 1-242, pls 1-38.

SEDIMENTOLOGY AND DEPOSITIONAL ENVIRONMENTS OF THE MIDDLE
DEVONIAN BIG BEND ARKOSE AND BURDEKIN FORMATION, FANNING RIVER
GROUP, BURDEKIN SUBPROVINCE, NORTH QUEENSLAND, AUSTRALIA.

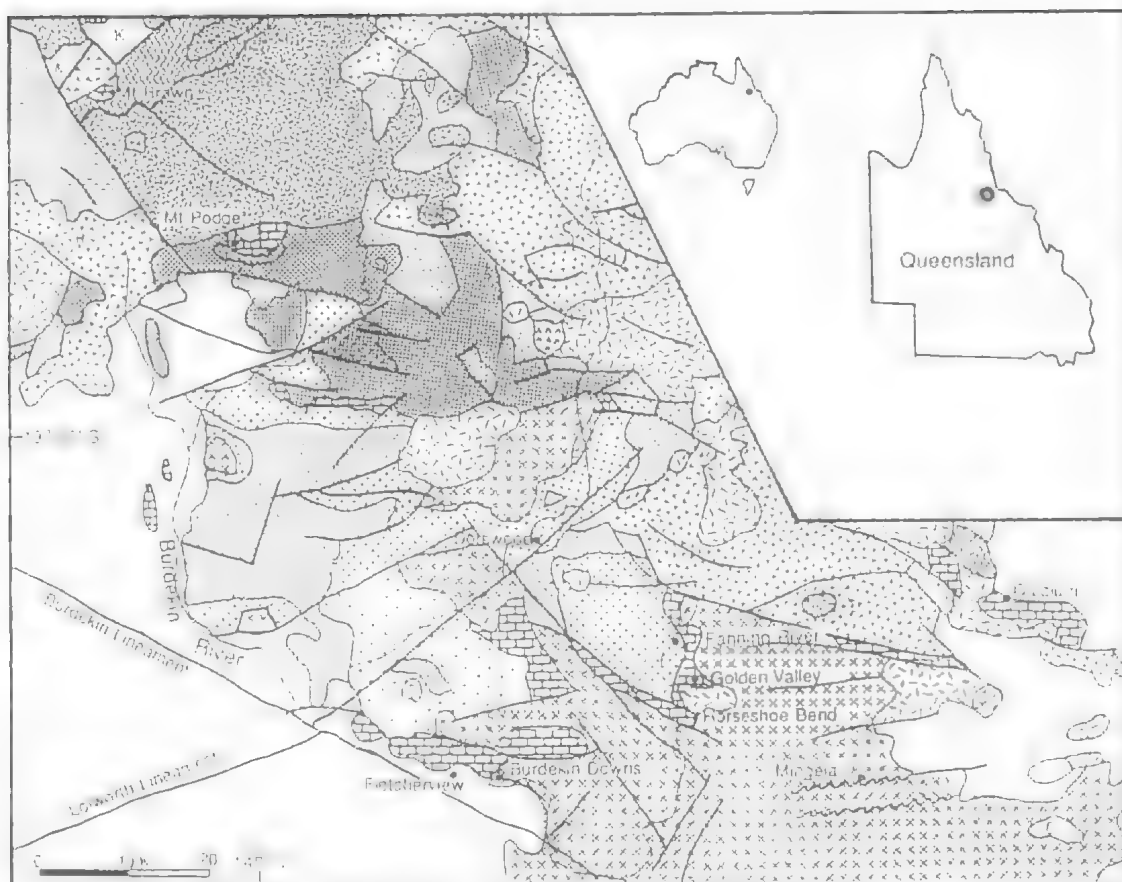
ALEX G. COOK

Cook, Alex G. 1995 06 01: Sedimentology and depositional environments of the Middle Devonian lower Fanning River Group (Big Bend Arkose and Burdekin Formation), Burdekin Subprovince, north Queensland, Australia. *Memoirs of the Queensland Museum* 38(1): 53-91. Brisbane ISSN 0079-8835.

Twelve distinct facies have been recognised for the Middle Devonian, (Erfelian-Givetian), Big Bend Arkose and Burdekin Formation of the Fanning River Group, Burdekin Subprovince, north Queensland. They represent deposition within the restricted Burdekin Basin in non-marine, shallow-water inner and proximal marine shelf, and shallow to moderate depth distal shelf environments. Non-marine deposition (unfossiliferous coarse siliciclastic facies) took place within restricted coastal plains, and represents coarse-grained channel and finer-grained floodplain deposits developed above *in situ* weathering profiles. Deposition within the inner shelf was complex, highlighting local influences of coarse siliciclastic input, inner shelf carbonate production and an across-shelf siliciclastic to carbonate transition. Facies deposited in the inner shelf were: (1) abraded coarse siliciclastic facies representing inundated marine headlands, and upper shoreface coarse siliciclastic deposition; (2) fossiliferous sandstone facies deposited in the subtidal lower shoreface; (3) fossiliferous siltstone facies, representing restricted fine-grained siliciclastic-dominated, nearshore, subtidal embayments; (4) nodular limestone facies deposited within mostly subtidal carbonate-dominated impure lagoons with local patch-reef development; and (5) impure limestone-sandstone facies representing sporadic deposition of mobile coarse siliciclastic sand bodies within an impure, subtidal carbonate lagoon. Deposition on the proximal shelf was dominated by stromatoporoid biostromal facies (seven divisions) representing biohermal (reefal) deposition (framestone), back reef and intrabiostromal stromatoporoid pavement (coverstone), interreef channel (grainy floatstone), extensive biostromes and storm-reworked equivalents which developed from the nearshore zone across the shallow shelf (silty rubbly floatstone, micritic stromatoporoid floatstone, rudstone, associated packstone and wackestone). Reef and biostromal growth took place with moderate levels of siliciclastic input, in proximity of granitic hinterlands and can be considered as preserved "fringing" reef and biostrome. Additionally, where extensive reef or biostrome did not develop, the proximal shelf was inhabited by dispersed stromatoporoid pavement (dispersed stromatoporoid packstone facies). Three facies represent distal shelf deposition, seaward of biohermal or biostromal growth: (1) coralline packstone, representing shallow water, offshore, coral and dendroid stromatoporoid thickets; (2) localised crinoid grainstone deposited as mobile carbonate sand bodies on the shallow distal shelf removed from significant siliciclastic input; and (3) micritic carbonate facies, restricted to the Golden Valley area, representing relatively deeper water deposition at the limits of the photic zone. *Endophyllum* siltstone facies represents growth of small coral-dominant patch reefs in a fine mixed carbonate-siliciclastic environment during initial stages of regression in the uppermost Burdekin Formation within the Fanning River area. Deposition of the lower Fanning River Group was controlled by basement topography and by the restricted nature of basin geography with significant variations across the subprovince. Two styles of shelfal assemblage developed, reflecting the development of a biohermal-dominated proximal shelf in the Fletcherview-Burdekin Downs area whereas in the Fanning River, Golden Valley, and Kirkland Downs areas a low relief biostromal-dominated proximal shelf assemblage developed. □ *Fanning River Group, Burdekin Formation, Big Bend Arkose, Devonian, Givetian, fringing reefs, sedimentology, stromatoporoids, biostromes.*

Alex G. Cook, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 12 December 1994.

The Fanning River Group is the lowermost stratigraphic unit of the Burdekin Subprovince, a Middle Devonian to Carboniferous succession WSW of Townsville, north Queensland (Fig. 1). The Fanning River Group was introduced by Wyatt et al. (1970) as consisting of three forma-



Legend

- | | |
|---|--|
| Cainozoic sediments, basalts and laterites | Late Devonian- Early Carboniferous Keelbottom Group and Collopy Fm (C) |
| Late Carboniferous to Early Permian intrusives | Late Devonian Dotswood Group |
| Late Carboniferous to Early Permian continental clastics Sybil Group (NW), Insolvency Gully (Central) | Middle Devonian Fanning River Group and Early Devonian carbonate- clastic assemblages |
| Late Carboniferous volcanics and volcanoclastics (E= Ellenvale Beds H= Hells Gate Rhyolite) | Camel Creek Subprovince Ordovician to Early Devonian massive carbonates and clastics (K) |
| Early Carboniferous Granites | Ravenswood Batholith |
| Early Carboniferous acid to basic volcanics (including Glenrock Group) | Precambrian Argentine Metamorphics |
| | Precambrian Running River Metamorphics (NW) and Kirk River Beds (E) |

FIG. 1. Geological map of the Burdekin subprovince, after Lang et al. (1990).

tions: Big Bend Arkose (dominantly coarse-grained siliciclastics), Burdekin Formation (a dominantly carbonate succession with some siliciclastic input) and Cultivation Gully Formation (a finer grained siliciclastic formation).

This paper is concerned with the sedimentology of constituent facies of the lowermost two formations of the Fanning River Group. The aim of the following sedimentological analysis is to provide an ecostratigraphic context for study of the abundant stromatoporoid fauna and other faunal elements (Cook, 1993a,b). This study also includes the Laroona Formation and Mt. Podge Limestone. These formations are older than the Fanning River Group, but represent a comparable sedimentary development and they are included for completeness. Stratigraphic sections were measured at sites identified for their stromatoporoid occurrence or sedimentological importance, and key sections were logged in detail with the collection of representative lithological and palaeontological samples. In addition several spot localities were examined where exposure was not conducive to stratigraphic logging.

The Big Bend Arkose and Burdekin Formation are herein divided into twelve facies grouped as non-marine, inner shelf, proximal shelf and distal shelf facies associations. A summary of the stratigraphic distribution of facies is presented in Fig. 2. The facies are briefly characterised, and their relationships determined, facilitating interpretation of the overall facies mosaic and depositional system. Detailed discussion of each facies follows, with inferred characteristics of the physical environment tabulated where possible. Detailed logs are available upon request from the author. Locality numbers used in this work refer to James Cook University of North Queensland register of fossil localities (see Appendix).

STRATIGRAPHY AND AGE

The name Big Bend Arkose was originally employed by Heidecker (1960), but formalised by Wyatt et al. (1970) who established the entire group. Burdekin Formation was an emendation of Burdekin Limestones (Leichhardt, 1847), Burdekin Downs Limestone (Jack, 1879a), Fanning River Limestone and Double Barrel Limestone (Jack, 1879b), Burdekin Beds (Jack, 1886) and Burdekin Formation (Jack and Etheridge, 1892). Wyatt et al. (1970) restricted the formation to the interval of calcareous shale, calcilutite, fossiliferous limestone, coquinite and minor

sandstone and shale interbeds above the Big Bend Arkose. They proposed the Cultivation Gully Formation for lithic sandstone and shale with calcareous, coralline interbeds in its lower part that conformably succeeds the Burdekin Formation. The type section for the Fanning River Group is located along the the Fanning River (L788) 3km upstream from Fanning River Station (L788) by Wyatt et al. (1970). Although the Big Bend Arkose and Burdekin Formation are thin and somewhat atypical at this site, it is by far the most complete, well-exposed section. Limited data is available on the precise zonal ages of the lower Fanning River Group. Problems arise from the paucity of conodont faunas in critical parts of the group and the biostratigraphic reliability of rugose corals and *Stringocephalus*.

Stringocephalus, traditionally regarded as the Givetian index fossil (cf. Zeigler, 1979) is common in the Fanning River area. Its lowest occurrence is 31m above the base of the group, and is abundantly present in a number of ecologically distinct horizons throughout this section. In addition, *Stringocephalus* is found near the top of the Burdekin Formation at Horseshoe Bend. These data strongly suggest a Givetian age for the bulk of the Burdekin Formation.

Rugose coral associations of Zhen (1991) from the Fanning River Group (excluding Mt. Podge), were given late Eifelian to middle to late Givetian ages. Zhen's (1991) "E" assemblage was given as *ensis* or slightly younger and is thus Givetian *sensu* Zeigler and Klapper (1985). Assemblage "G", was assigned a late Eifelian to early Givetian, this partially related to the presence of *Stringocephalus*, 60m above the lower limits of assemblage "G". As previously stated, *Stringocephalus* has been subsequently recorded lower in the sequence, in the middle of assemblage "G" of Zhen (1991). A Givetian age for Assemblage "G" is therefore favoured.

Conodont data for the Burdekin Formation are limited. Conodonts indicative of *varcus* zone age were reported by Zhen (1991) from Turtle Creek in the NE of the Subprovince. Limited conodont data has become available on the age of the Burdekin Formation and the Mount Podge sequence from the work of Talent & Mawson (1994). Material processed from the Fanning River type section, Kirkland Downs and Burdekin Downs yielded conodonts which indicate a predominantly Givetian age for the sequence. Conodonts within the upper two thirds of the type section are of middle to late *varcus* age (Talent & Mawson, 1994). This conclusion combined with

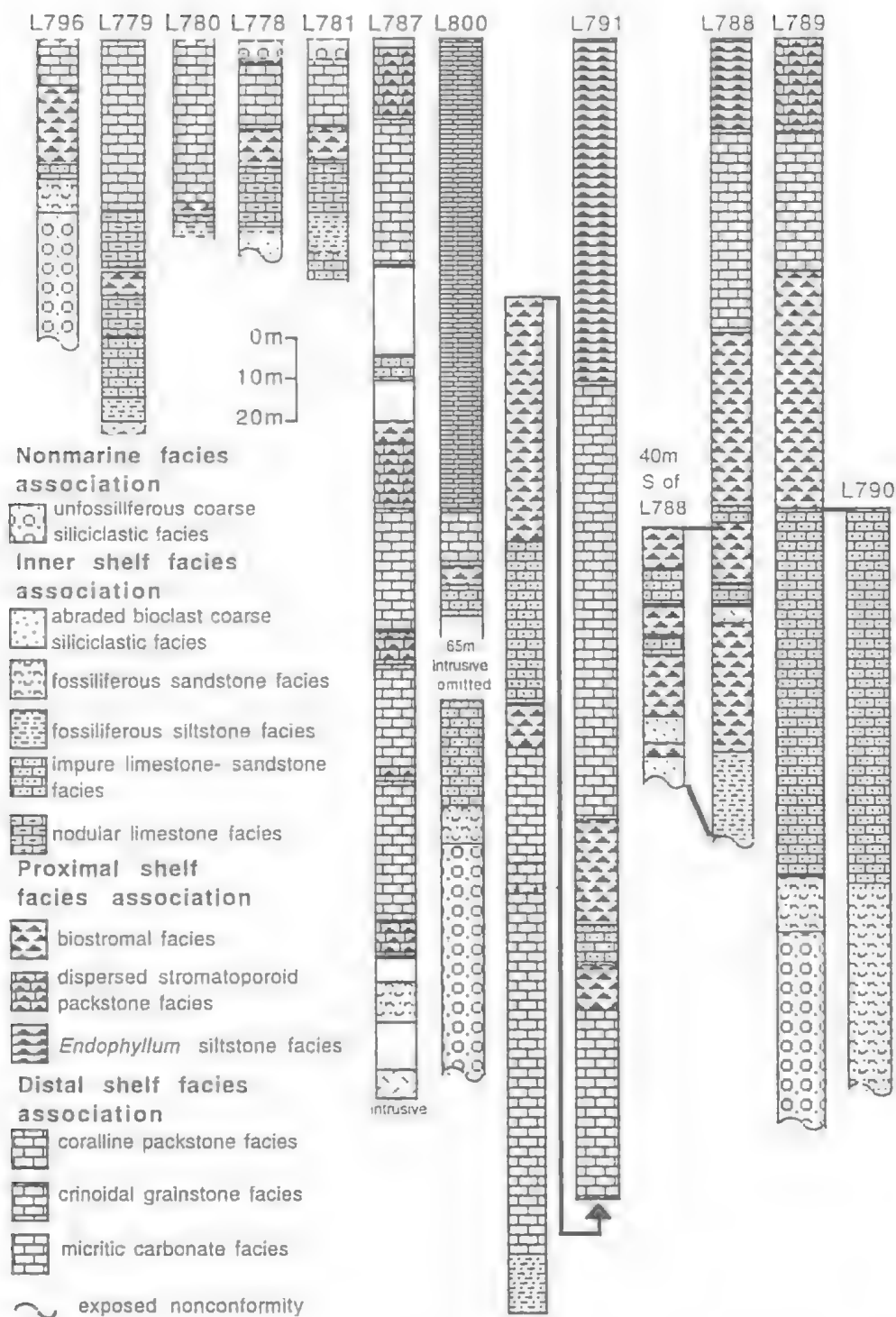


FIG. 2. Facies associations in principle sections for the lower Fanning River Group. For localities refer to Appendix.

the occurrence of *Stringocephalus* extends Givetian ages down to 31m above the unconformity within the Fanning River type section (Talent & Mawson, 1994). This suggests that all of the type section is likely to be of Givetian age. At Kirkland Downs the majority of the sequence lies within the *ensensis* zone, probably late *ensensis*, with upper section within the early *varcus* zone. Limited data from Burdekin Downs suggest a pre-late *varcus* age for at least the lower half of the sequence. Conodonts from Mount Podge show an Emsian-Eifelian age ?late *inversus-serotinus* to *costatus* zones, for most of the succession. A Givetian age, at least early *varcus* zone is indicated for uppermost units in one western Mount Podge section (Talent & Mawson, 1994).

In summary, the age of the Big Bend Arkose and the lower parts of the Burdekin Formation may range into the Eifelian, but most of the Burdekin Formation is of Givetian age with its uppermost sequences ranging into the late *varcus* zone, or perhaps younger.

TERMINOLOGY

Nomenclature of coarse siliciclastics is from Folk (1974) whereas carbonate dominated lithologies are named using the textural classification of Dunham (1962) with modifications from Embry and Klovan (1971) and Tsien (1981). For carbonate-siliciclastic mixtures it is desirable to identify amounts of impurity. Prefixes are applied to carbonate lithologies indicating the percentage range of siliciclastic impurities as follows:

- 0-5% -carbonate name only
- 5-10% -slightly impure
- 0-30% -moderately impure
- 30-50% -highly impure.

The grain size of the siliciclastic fraction is also indicated. Examples of this approach are "slightly impure fine sandy wackestone" and "highly impure silty floatstone". These terms are also applied to the matrices of boundstone lithofacies to provide a gross guide to the elastic signature of stromatoporoid-bearing lithologies. Siliciclastic-dominated lithologies within the sequence commonly have a significant fossil content. The following prefixes are used as an indication of this:

- 2-10% -slightly fossiliferous
- 10-30% -moderately fossiliferous
- 30-50% -highly fossiliferous.

The word "biostrome" has both a sedimentological and palaeoecological meaning. Its sedimentological use denotes a bedded deposit

constructed largely by living organisms and its palaeoecological sense it implies a flat bottomed, low relief community of benthic organisms.

FACIES RELATIONSHIP TO LITHOSTRATIGRAPHY

The contact between the Big Bend Arkose and Burdekin Formation is transitional, and a precise facies boundary between the two cannot be defined. In general however the facies associations can be divided into:

Big Bend Arkose

- Unfossiliferous coarse siliciclastic facies
- Abraded bioclast coarse siliciclastic facies
- Fossiliferous sandstone facies

Burdekin Formation

- Fossiliferous siltstone facies
- Impure limestone-sandstone facies
- Nodular limestone facies
- Biostromal limestone facies (seven divisions)
- Endophyllum* siltstone facies
- Dispersed stromatoporoid packstone facies
- Coralline packstone facies
- Crinoidal grainstone facies
- Micritic carbonate facies

FACIES ASSOCIATIONS OF THE BIG BEND ARKOSE AND BURDEKIN FORMATION

NON-MARINE ASSOCIATION

- Unfossiliferous coarse clastic facies (Table 1)

DIAGNOSIS

Localised granitic boulder conglomerate resting on weathered and jointed granitoid basement, or metamorphic cobble conglomerate resting on metamorphic basement. Thick-bedded, unfossiliferous, trough and planar cross-laminated coarse sandstone sporadically interbedded with red or purple sandy siltstone.

DISTRIBUTION AND THICKNESS

FANNING RIVER NORTH: L789; 20m of section consisting of basal conglomerate, interbedded red siltstone and coarse arkosic sandstone. FANNING RIVER CAVES AREA: immediately N of base of section. L791; scattered outcrops of red siltstone and coarse arkose. GOLDEN VALLEY NORTH: L800; approximately 45m thick, <1m basal conglomerate, 5-10m pebbly granule-rich arkosic sandstone and approx 35m of coarse sub-arkose. ARTHURS CREEK TRIBUTARY: L783; approximately 13m of thin basal conglomerate, over-

TABLE 1. Characteristics of the non-marine facies association. C= common, A= abundant.

| NON MARINE FACIES ASSOCIATION | | | | |
|---|---|--|--|--|
| Facies | Unfossiliferous coarse siliciclastic facies | | | |
| Lithology | conglomerate | | sandstone | siltstone |
| | granitic clast | metamorphic clast | | |
| Bedding massive (M), very thick (v), thick (T), medium (m), Thin (h) | M, V-T | M, V-T | M, V-m | M, T-h |
| planar cross bearing trough X bedding planar lamination ripple X lamination | | Crude Minor Crude Imbrication | A C A C | C |
| Nodules | | | | carbonate |
| Grain sizes | cobble-boulder | msand-large cobble | fsand-granule, sporadic pebbles | |
| | sandy or silty mix | sandy or silty mix | | |
| | granite clasts | metamorphic clasts, qtz | Arkose: qtz, felds, bio, hbl, rare aplite rfs, granite rfs | clays, qtz, bio, felds |
| | qtz, felds, bio, qrf in mtx | qtz, felds, bio, muscovite, rfs in mtx | Litharenite: muscovite, biotite, qtz, metamorphic rfs | |
| Fabric | clast supported, unsorted | | poorly-moderately sorted | |
| Lithology | oligmict conglomerate | | arkose-subarkose metalitharenite | siltstone-sandy siltstone |
| Other features | both lie upon jointed basement | | | Plant fossils reported by Wyatt (1973) from Turtle Creek |

lain by red sandy siltstone succeeded by coarse subarkosic sandstone. KIRKLAND DOWNS: L798; approximately 35m of interbedded litharenite, sublitharenite and subordinate green and purple micaceous siltstone. MOUNT PODGE: L801; approximately 5m of trough cross bedded, metamorphic-derived conglomerate overlain by approximately 5m granule-pebble conglomerate.

DESCRIPTION

This facies rests nonconformably on basement and consists of boulder to cobble conglomerate, red-coloured shale and sandy siltstone, and coarse arkose or metalitharenite. Granitic boulder conglomerate lies atop progressions from jointed basement, through weathered corestone fabric to boulder conglomerate supporting a silty or sandy arkosic matrix. The conglomerate intervals are thin, rarely more than 5m thick, and are poorly exposed and locally restricted. Metamorphic conglomerate is thinner, and unconformably overlies analogous, but much thinner, progressions from basement. It often show trough cross bedding and imbrication. Sandstone, which dominates the facies is thickly bedded, commonly planar and trough cross bedded, unfossiliferous coarse

arkose or micaceous litharenite. Poorly outcropping, laminated sandy siltstone is uncommon as interbeds and very rarely contain small carbonate nodules.

DISCUSSION

Terrestrial unconformities upon crystalline basement are commonplace in the modern environment, but ancient examples have been rarely reported in the literature (Wahlstrom, 1948; Williams, 1968; Went, 1991). Went (1991) described similar features for early Palaeozoic unconformities, noting corestone fabrics developed upon coarse igneous basement which he interpreted as representing weathering profiles. The progression up-section into the basal Big Bend Arkose indicates a penecontemporaneous (Devonian) weathering profile upon the Ravenswood Granodiorite complex and Argentine Metamorphics.

Conglomerates and other coarse clastics are interpreted as fluvial on the basis of the absence of marine fossils, so abundant in immediately adjacent facies, proximity to basement and localised distribution, and the presence of planar and trough cross beds (Walker, 1984). Siltstones

are interpreted as related "floodplain" deposits. Rare carbonate nodules may be reworked caliche nodules, indicative of pedogenesis in arid, hot conditions (Allen, 1974).

The facies represents the *in situ* development of a weathering profile on granitic or metamorphic basement, and coarse pebbly sandstones or pebble conglomerates of fluvial origin deposited on restricted coastal plains in response to rising sea-level.

INNER SHELF AND SHOREFACE ASSOCIATION

Abraded bioclast, coarse siliclastic facies (Table 2)

DIAGNOSIS

Localised granitic boulder conglomerate with interstitial sandstone containing abraded or rarely *in situ* fossils overlying jointed and weathered basement. Coarse sandstone, planar or cross-laminated contain abundant abraded bioclasts.

DISTRIBUTION AND THICKNESS

FANNING RIVER: L788; approximately 5m of basal granitic conglomerate and <1m of coarse subarkose; adjacent section contains two 5m units of medium bedded coarse moderately fossiliferous subarkose separated by a 2.5m biostromal rubble unit. HORSESHOE BEND: L786; 4m of granitic conglomerate succeeded by 2.5m of fining-upwards, medium bedded, moderately fossiliferous subarkose. FLETCHERVIEW: L788; 3m basal granitic conglomerate with silty matrix overlain by a thin unit < 0.8m of thickly bedded coarse-grained, moderately fossiliferous subarkose. L779; 1.7m of thickly bedded moderately fossiliferous pebble conglomerate and very coarse-grained subarkose. BURDEKIN DOWNS: L783; 2m of granitic boulder conglomerate with interstitial encrusting and unabraded fossils within coarse arkosic matrix. Overlying outcrop obscured. HERVEYS RANGE: <5m of moderately fossiliferous metamorphic cobble conglomerate. MOUNT POGGE, approximately 10m coarse-grained, slightly fossiliferous coarse to medium grained sublitharenite. Some units referred to the fossiliferous sandstone facies at Fanning River North and Golden Valley are transitional to the abraded bioclast, coarse siliclastic facies.

DESCRIPTION

The facies is characterised by coarse clastic units containing an abundance of abraded bioclasts. Thin, locally restricted, granitic boulder conglomerate contains common to abundant, abraded fossil bioclasts and rare limestone intraclasts within a dominantly coarse arkosic, or less commonly siltstone matrix (Fig. 3A). These

units nonconformably overlie a basement progression akin to that described for the unfossiliferous coarse clastic facies. At L793, granitic boulders display an encrusting fauna of *Stachyodes* and *Alveolites*, and at L786 non-abraded coralline and dendroid stromatoporoids are found in boulder interstices. The facies is dominated by thick bedded slightly to moderately fossiliferous coarse-grained arkose, commonly with sets of low-angle cross and planar laminae. Abraded bioclasts include gastropods, bivalves, abundant tabulate and rugose coral debris and dendroid stromatoporoid debris.

DISCUSSION

Granitic conglomerates represent *in situ* progressions from jointed basement through spheroidally weathered granitoid to boulder conglomerates showing no sign of transport. They are interpreted as rocky headlands or palaeorupicost (Johnson, 1988a) preserved due to rapid transgression accompanying rapid deposition. Lateral relationships indicate a pre-weathered surface which does not fit Johnson's (1988b) genetic classification of rocky shorelines. Preponderance of broken and abraded bioclasts within the matrix suggests intertidal reworking, but encrusting *Stachyodes costulata*, foliose *Alveolites* sp., and non-abraded specimens of the same taxa indicate the continuance of headland bedrock into the subtidal zone. Close vertical and lateral associations with sandstone units suggests continuity with high energy sand deposition adjacent to such headlands. Coarse arkose is interpreted as a shoreface deposit on the basis of abundant broken bioclasts, presence of low angle cross lamination, planar laminae and proximity to basement. These features are consistent with upper shoreface deposition, transitional to lower shoreface, well above fairweather wave base (Reineck and Singh, 1980; Walker, 1984; Reinson, 1984). The facies represents localised rocky marine headlands (rupicost) and associated shoreface deposition.

Fossiliferous sandstone facies (Table 2)

DIAGNOSIS

Thick-bedded, coarse-grained, fossiliferous sandstone containing an abundant molluscan fauna in addition to slightly abraded coralline bioclasts. Uncommon, thin siltstone interbeds are bioturbated and contain an abundant unabraded coralline fauna.

TABLE 2. Characteristics of coarse siliciclastic facies of the inner shelf facies association. Letter in bold= *in situ*, italicised= fragmental and transported, plain text= reoriented or unabraded. R = rare, U= uncommon, C= common, A= abundant.

| INNER SHELF FACIES ASSOCIATION | | | | | |
|---|---|-----------------|--------------------------------|------------------------------|-------------------------|
| Facies | Abraded bioclast, coarse clastic facies | | Fossiliferous sandstone facies | | |
| Lithology | conglomerate | sandstone | sandstone | siltstone | mudstone/ wackestone |
| Fauna | | | | | |
| Stromatoporoids | | | | | |
| laminar | <i>U</i> | <i>R</i> | <i>R</i> | <i>U</i> | <i>U</i> |
| low-medium domical | <i>U</i> | <i>R</i> | <i>R</i> | <i>U</i> | <i>U</i> |
| high domical-bulbous | <i>U</i> | <i>R</i> | <i>R</i> | <i>U</i> | <i>U</i> |
| dendroid | R U U | <i>R</i> | <i>R</i> | R U | R U |
| Tabulate corals | | | | | |
| ramose alveolitids | R U | <i>R</i> | | R U | R U |
| auloporids | | | | <i>U</i> | <i>U</i> |
| <i>Heliolites</i> | <i>U</i> | <i>R</i> | <i>R</i> | <i>R</i> | <i>R</i> |
| domical alveolitids | R U | <i>R</i> | <i>R</i> | <i>R</i> | <i>R</i> |
| foliose alveolitids | R U | <i>R</i> | <i>R</i> | <i>R</i> | <i>R</i> |
| Rugose corals | | | | | |
| solitary (small) | <i>U</i> | <i>R</i> | <i>U</i> | <i>C</i> | <i>C</i> |
| colonial | | | | | |
| solitary (long/delicate) | | <i>R</i> | <i>R</i> | <i>R</i> | <i>R</i> |
| Chaetetids | <i>R</i> | <i>R</i> | <i>R</i> | <i>R</i> | <i>R</i> |
| Bivalves | <i>C</i> | <i>C</i> | A A | A A | A A |
| Nautiloids | | | | | <i>R</i> |
| Gastropods | <i>C</i> | <i>C</i> | A A | A A | A A |
| Crinoids | | | <i>R</i> | <i>R</i> | <i>R</i> |
| Brachiopods | <i>R</i> | | <i>R</i> | <i>R</i> | <i>R</i> |
| Bedding features | | | | | |
| massive (M), very thick (v), thick (T), medium (m), thin (h) | M | M, V - m | M, V - m | T - m | T - m |
| planar cross bedding | | <i>C</i> | <i>C</i> | | |
| planar lamination | | <i>C</i> | <i>C</i> | C FINE | <i>U</i> |
| planar X lamination | | <i>C</i> | <i>C</i> | | |
| ripple X lamination | | | | <i>U</i> | <i>R</i> |
| Nodules | | Some Fe | Some Fe | <i>C</i> | <i>C</i> |
| Stylolites; low sinuosity | | | | <i>C</i> | <i>C</i> |
| Grain sizes | | | | | |
| clastics | boulder to cobble with vcsand or silty mix | fsland-pebble | to vcsand | to vcsand | to vcsand |
| carbonates | to cobble | to cobble | to cobble | to cobble | to cobble |
| Bioturbation | | | many burrows and traces | extensive | extensive |
| Clastic grain types | dependant upon basement: granitic basement: granitoid, feldspar, qtz, biotite, tourmaline, homblende. metamorphic basement: meta r.f.s. qtz, muscovite, biotite | | | qtz, felds, biotite dominant | |
| Impurity | | | | | up to 50% |
| Other features | rare intraclasts | | | | |

DISTRIBUTION AND THICKNESS

FANNING RIVER NORTH: L789; 10m of medium to thickly bedded subarkose interbedded with sandy siltstone, minor carbonate mudstone interbeds near the top, all moderately fossiliferous. L790; 46m of coarse-grained subarkose interbedded with sandy calcareous siltstone towards the top, all moderately fossiliferous. FANNING RIVER CAVES: L791; approximately 15m of thickly bedded, slightly to moderately fossiliferous coarse-grained subarkose. GOLDEN VALLEY NORTH: L800; approximately 8m of thickly bedded coarse subarkose with minor interbedded impure sandy packstone near top. KIRKLAND DOWNS: L796; approximately 8m of thickly bedded fossiliferous coarse sublitharenite. PAYNES LAGOON: approximately 80cm of moderately fossiliferous sublitharenite.

DESCRIPTION

This facies is dominated by thick-bedded, commonly cross bedded, coarse-grained, fossiliferous arkose which is generally displays fine to medium laminae and cross laminae and contains an abundant gastropod and bivalve fauna, in addition to abraded coralline debris. Less common, thin, moderately fossiliferous sandy siltstone interbeds show bioturbation and contain common coralline bioclasts showing limited abrasion. Interbeds of moderately impure silty to sandy mudstone and wackestone are common in the upper part of the association. They contain a scattered coral, dendroid stromatoporoid and molluscan fauna.

DISCUSSION

Unless storm-generated, large coarse-grained sand bodies are restricted to above fairweather wave base which generally falls within 5-15m below sea level (Walker, 1984). Abundance of low angle cross lamination, and *in situ* molluscan and coralline fauna suggest deposition of active mobile sand bodies on the lower shoreface, above fairweather wave base, but below the mean low water mark. A location on the innermost shelf, in very shallow water is indicated. Given the probable small fetch of the Burdekin Subprovince, discussed later, fairweather wave base may have been unusually shallow and a 5m depth is probably a maximum figure. These sand bodies are interpreted to be channel mouth bars and associated merged sheet sands from creeks analogous to small, simple birdsfoot deltas (Walker, 1984; Miall, 1984). A limited distribution reflects basement topography and the position of stream outfalls. Given basement topography, these units may represent mid to distal parts of small fluvial channels bordering the basin which encroach into the shallow marine environment, such as those

described by Roberts & Murray (1988) from the northern Red Sea. Transition to the overlying muddier, carbonate-dominant facies represents facies mixing (Mount, 1984) and records a gradation to sheltered subtidal lagoonal environments generally below fairweather wave base.

Fossiliferous siltstone facies (Table 3)

DIAGNOSIS

Thin-to medium-bedded, bioturbated, sandy siltstone, with sandstone lenticles and stringers, contains an abundant ramose coralline and a shelly fauna. A stromatoporoid biostrome is present at one studied locality. Highly impure wackestone and packstone are common in the upper stratigraphic intervals of the facies.

DISTRIBUTION AND THICKNESS

FANNING RIVER: L788; approximately 15m of sequence, laterally discontinuous, consisting of fossiliferous medium to thin bedded, laminated, nodular siltstone with abundant corals, common sandy stringers and a singular diffuse stromatoporoid biostrome. FLETCHERVIEW: L779; approximately 6m of interbedded siltstone, nodular calcareous siltstone and wackestone with common sandy stringers, abundant coral, *Stachyodes* and molluscan fossils. Minor fenestral limestone. L780; 3m of increasingly calcareous and fossiliferous micaceous siltstone with abundant coral and mollusc fauna. L778; <1m of siltstone beds, abundant coralline fauna, transitional to overlying nodular limestone. BURDEKIN DOWNS: L781; 10m of siltstone interspersed with silty coralline packstone and wackestone, rare sandy stringers all with abundant coral and *Stachyodes* fauna, transitional to overlying nodular limestone association.

DESCRIPTION

This facies consists of thin to medium bedded, laminated, nodular, extensively bioturbated calcareous or sporadically carbonaceous, fossiliferous sandy siltstone containing an abraded and non-abraded branching tabulate coral, solitary rugose coral and molluscan assemblage. Silty sandstone occurs as lenticular stringers or thin to medium bedded, bioturbated, fossiliferous units. Carbonate mudstone and wackestone are moderately impure, becoming more dominant up sequence. These are likewise bioturbated and contain a ramose tabulate and rugose coral fauna. At Fletcherview (L779) algal, laminated, impure limestone is found in one horizon, displaying a weak fenestral fabric. Localised packstone patches are common in impure limestone units. At Fanning River, an unbound stromatoporoid

TABLE 3. Characteristics of inner shelf facies associations; fossiliferous siltstone and impure limestone facies. Letter in bold= *in situ*, italicised= fragmental and transported, plain text= reoriented or unabraded. R= rare, U= uncommon, C= common, A= abundant, D=dominant. # includes rare *Stringocephalus*.

| INNER SHELF FACIES ASSOCIATION | | | | | | |
|--|--------------------------------------|--------------------|-----------------------|--|---------------------|-----------------------|
| Facies | Fossiliferous siltstone facies | | | Impure limestone-sandstone facies | | |
| Lithology | siltstone | wackstone-mudstone | biostrome | sandstone | wackestone mudstone | coquinite |
| Fauna | | | | | | |
| Stromatoporoids | | | | | | |
| laminar | U U | | A | C | | |
| low-medium domical | U U | | A | C | | C |
| high domical-bulbous | U U | | A | | | |
| dendroid | U | C | U | U | CC | U |
| Tabulate corals | | | | | | |
| ramose alveolitids | D D | C C | | C | C C | C |
| auloporids | C | C C | C | | C C | |
| <i>Heliolites</i> | C C | C C | U | C | C C | U |
| domical alveolitids | C C | C C | C | C | C C | U |
| foliose alveolitids | C C | R R | U | C | R R | |
| Rugose corals | | | | | | |
| solitary (small) | A A | A A | C | C | A A | |
| solitary (long/delicate) | U U | U U | | U | U U | |
| Chaetetids | C | R | | | R | |
| Bivalves | C C | C C | | C | C C | D D |
| Nautiloids | R | R | | | R | |
| Gastropods | C C | C C | | C C | C C | C C |
| Crinoids | U | U | | | U | |
| Brachiopods | C C l. | C C | | | C C | U |
| Bedding features | | | | | | |
| massive (M), very thick (v), thick (T), medium (m), thin (h) | H - m | m - T | | V - T (sometimes graded) | m - T | m - T |
| planar cross bedding | | | | C | | C |
| planar lamination | C FINE | U FINE | | C | U FINE | C |
| planar X lamination | | U | | C | U | C |
| ripple X lamination | U | U | | | C | |
| Nodules | A | A | | A (Fe nodules) | A | A (Fe nodules) |
| Low sinuosity stylolites | A | A | U | | A | |
| Grain sizes | | | | | | |
| clastics | silt-vesand | silt-vesand | | csand-granule | silt-vesand | med sand-small pebble |
| carbonates | mud cobble | mud cobble | | msand-cobble | mud-cobble | msand-cobble |
| Bioturbation | extensive | extensive | | many burrows and traces | extensive | extensive |
| Clastic grain types | qtz, feldspar, biotite, granitic rfs | | | qtz, feldspar, hornblende, granitic rfs, metamorphic rfs, biotite, muscovite, tourmaline | | |
| Impurity | clastic rock | up to 50% | | clastic rock | up to 50% | up to 50% |
| Carbonate fabric | n.a. | above | restricted bindstones | n.a. | above | grainstone |

biostromal unit occurs as a lenticular body within the fossiliferous siltstone facies.

DISCUSSION

Ubiquitous bioturbation, the dominance of branching corals and stromatoporoids, and the fine grained signature suggests a quiet water, fine siliciclastic, inner shelf depositional environment (Enos, 1983; Belperio & Searle, 1988; Flood & Orme, 1988) either below fairweather wave base or protected from wave energy by offshore biostromal or biohermal barriers. Whereas some sedimentary structures are preserved most have been obliterated by bioturbation and this is typical, but not diagnostic, of inner shelf subtidal deposition (Enos, 1983). Lateral discontinuity at Fanning River implies embayment deposition, whereas more extensive development near Burdekin Downs suggests a broader subtidal siliciclastic zone. Sand stringers represent minor storm admixtures to this subtidal domain (Walker, 1984). The abundance of barely abraded ramose tabulate and solitary rugose corals highlights a dispersed subtidal coralline community. The toppling and some breakage of the ramose coralline fauna suggests some periods of relatively elevated energy conditions such as those induced by storms, but deposition was mostly sheltered from high energy events.

The stromatoporoid biostrome at Fanning River within this facies must have been subtidal in its development. Growth forms of the fauna within this biostrome show a response to fine clastic input (stress?) with multiple overgrowths of stromatoporoids and tabulate corals. By analogy to modern subtidal bay muds and muddy sands on the north Queensland shelf, which extend to the mean low spring tide mark (Belperio & Searle, 1988) water depths for this association can be estimated as probably less than 5m below mean low water mark.

Fenestral limestone found only at the base of the association at L779 is similar to that described by Laporte (1967) and Read (1973) and indicates supratidal exposure as a minor perturbation of local sea level or tectonic adjustments.

Impure limestone-sandstone facies (Table 3)

DIAGNOSIS

Thick-bedded, commonly cross-laminated coarse sandstone is interbedded with variably impure carbonate mudstone and wackestone.

Minor coquinite (coarse, sandy bivalve grainstone) is likewise cross-laminated.

DISTRIBUTION AND THICKNESS

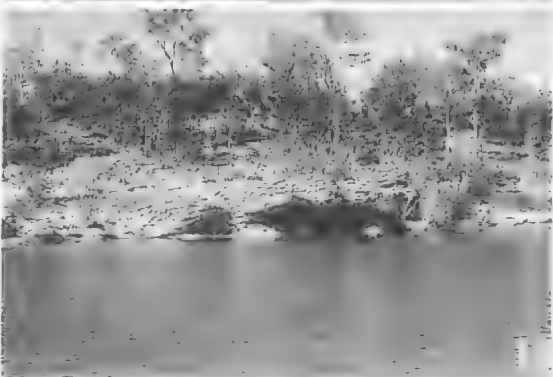
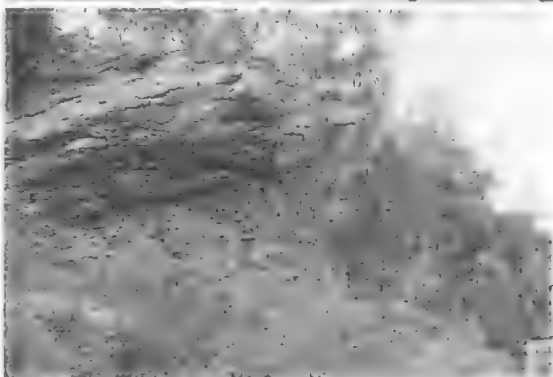
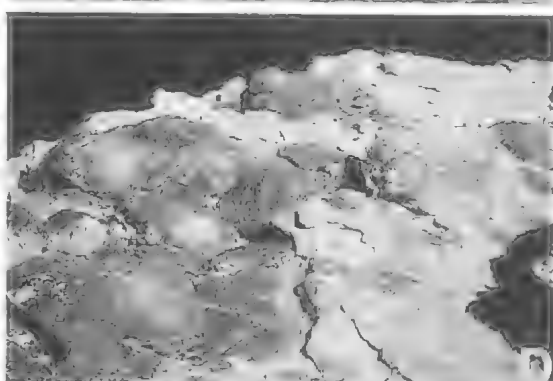
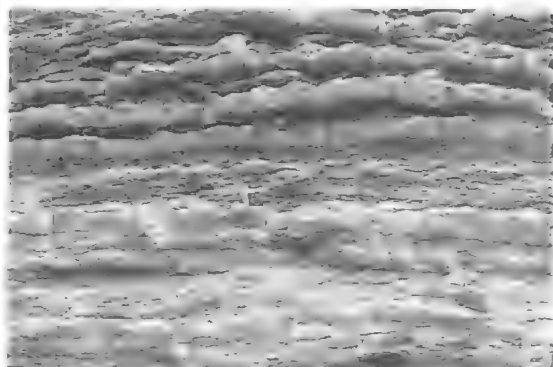
FLETCHERVIEW: L779; 14.5m thick, with basal molluscan packstone coarsening upwards to coquinite, interbedded coarse sandstone, impure wackestone, packstone and carbonate mudstone. BURDEKIN DOWNS: L781; approximately 4m of poorly outcropping coarse sandstone beds with interbedded impure packstone, L784; 8m of impure sandy wackestone and packstone with coarse sandstone interbeds. GOLDEN VALLEY: L800; approximately 30m of poorly outcropping impure wackestone, packstone and coarse siliciclastic sandstone interbeds. HORSESHOE BEND: L787; very poorly outcropping sandy packstone, of indeterminate thickness. FANNING RIVER CAVES: L791; three packages, all poorly exposed, of interbedded coarse siliciclastic sandstone and sandy packstone and wackestone. FANNING RIVER: L 788; and environs; two packages <4m thick of relatively poorly outcropping, fossiliferous coarse siliciclastic sandstone, sandy packstone and wackestone. FANNING RIVER NORTH: L789, L790; approximately 80m of interbedded coarse sandstone, sandy and silty wackestone and packstone.

DESCRIPTION

Coarse terrigenous units interbedded with sandy to silty impure pellet grainstone, wackestone and mudstone are characteristic. Coarse, slightly fossiliferous arkose packages are thick to medium bedded, commonly show low angle cross laminae, sporadically display a lobate plan geometry, and are somewhat discontinuous. Bivalve coquinites (highly impure molluscan grainstones) are present at several localities. Impure, thinly laminated silty and sandy limestone is ubiquitously bioturbated, pelletal and contains an abundant fauna of fragmental and unabraded coral, stromatoporoid and molluscan remains. Pellet grainstones are bioturbated but laminae and cross laminae are commonly preserved. Carbonate mudstones are variably impure, and display vertical burrows as part of extensive bioturbation.

DISCUSSION

The juxtaposition of coarse terrigenous sediments with muddy, albeit impure, carbonates suggests an environment of fluctuating energy. Carbonate lithologies are similar in depositional style to those of the nodular limestone association discussed below. Abundant bioturbation, minor planar lamination and cross lamination, and a delicate fauna coupled with the absence of fenestral limestones supports interpretation as an imp-



ure muddy carbonate lagoon with water depths of only a few metres (Read, 1973; Hardie & Ginsburg, 1977; Enos, 1983). Toppling and some breakage suggests episodic storm activity.

Sandstones are interpreted to represent mobile sand bars derived from stream outfall which prograded across the adjacent lagoonal floor during periods of high runoff. Interbedding suggests that each unit represents a channel outflow from a small delta or wadi system (cf. Roberts & Murray, 1988) and that the distributary channel or equivalent avulsed (Miall, 1984).

Intercalation of coarse siliciclastic and carbonate lithologies has been reported by a number of authors (Read, 1973; Freidmann, 1988; Roberts, 1987), generally in the context of intertidal to supratidal sediments. Interbedding is considered to result from sporadic, intense events which transport coarse siliciclastics into the marine environment (Roberts & Murray, 1988). Modern nearshore, backreef lagoons are known to contain mobile sand bars, coral pavements and patch reefs (Roberts & Murray, 1988).

Coquina beds, especially those evident at Fletcherview L779, were deposited as a coarsening upwards sequence prior to the deposition of other associational elements. Coarsening upwards trends, the disarticulated state of bivalves and bioturbation especially of lower beds suggests increasing energy of deposition from a relatively quiet lagoonal subtidal floor to high energy, current driven, bivalve-rich, sand bodies. The bivalve debris were likely to have been derived from within the lagoon.

Nodular limestone facies (Table 4)

DIAGNOSIS

Bioturbated, nodular, impure mudstone and wackestone which contains a scattered, but abundant, dendroid coralline fauna, with patch reefs developed within the upper stratigraphic levels of the facies.

DISTRIBUTION AND THICKNESS

FLETCHERVIEW: L778; 9m of nodular mudstone and wackestone with scattered dendroid fauna and patch bioherms overlying a conglomeratic unit in upper 2m. L779; 7m of section below the biohermal facies, with rare low patch bioherms; some 5m above somewhat impure coral-*Amphipora* rich wackestone-packstone. L780; approximately 2m of nodular lime mudstone and limey mudstone with patch bioherms. BURDEKIN DOWNS: L781; approximately 12m of somewhat impure nodular wackestone containing a biohermal unit in upper part, and minor sand beds in lower part. HORSESHOE BEND: L786; approximately 6m of relatively pure wackestone.

DESCRIPTION

The facies is dominated by thick to medium bedded, nodular mudstone with wackestone patches (Fig. 3B), and diffuse, commonly pelletal, wackestone units containing dendroid stromatoporoids (*Stachyodes*), solitary rugose corals, branching tabulate corals, rare isolated low domical to medium domical chaetetids, stromatoporoids, abundant bivalve hash, and sporadic nautiloid remains. The units are slightly to moderately impure, with siliciclastic impurities consisting of clay, silt and fine sand. Isolated patches of framestone, comprising microatolls or patch reefs up to 1.5m in height (Fig. 3C,D,E), contain low domical to medium domical stromatoporoids, tabulate corals, and have a halo of dendroid stromatoporoids, fasciculate tabulate corals and solitary rugose corals. They take two forms: low diffuse framestone-coverstone patches or bulbous to columnar stacks of framestone. A singular conglomerate unit in the Fletcherview (L778, 780) area is thin and poorly sorted, consisting of granule to pebble sized clasts of coralline debris, granodiorite and minor mudstone intraclasts in a coarse arkosic sandstone matrix.

The nodular fabric characteristic of this facies is a variable feature ranging from isolated lenticular pods up to 60cm in length within a more silty matrix to rather homogenous mottled limestone characterised by irregular bedding surfaces. Although highly variable, the general trend is from isolated nodules in the lowermost parts of the

FIG. 3. A, rounded granitic boulder conglomerate upon unconformity surface at Fletcherview Station L778. Hammer for scale. B, nodular limestone association showing upwards increase in proportion of limestone units. Fletcherview Station L778. C, E, bulbous-like patch reefs within nodular limestone association at Fletcherview Station L778. D, upper surfaces of coverstone style patch reefs within nodular limestone association at L778. F, Lower biostromal association, Burdekin River L781 showing transition from well bedded nodular limestone to laminar stromatoporoid coverstone to framestone. G, framestone outcrop, Burdekin River L781. H, prominent outcrops of framestone L781.

facies progressing through low sinuosity, coalesced nodules to homogenous mottled limestone in the uppermost parts of the facies. Typically nodular limestone is succeeded by biostromal facies but some sequences (L781, L779) show the opposite pattern.

DISCUSSION

The facies is interpreted to have been deposited in an inshore sheltered lagoon, mostly removed from destructive wave energy and coarse clastic input, below normal wave base and away from stream outfall. Ubiquitous bioturbation which has resulted in the loss of sedimentary structures, coupled with the abundance of dendroid coralline forms supports this interpretation (Hardie & Ginsburg, 1977; Enos, 1983; Bjerstedt & Feldmann, 1985; Harrington, 1987). The toppling and limited reworking of dendroid forms resulted from episodic increases in current energy, probably related to storms, but this was insufficient to displace larger isolated domical coral and stromatoporoid forms. The presence of some ripple cross lamination in pelletal sediments and limited preferential orientation of *Stachyodes* sp. adjacent to patch reefs also attests to some current activity.

The localised conglomerate unit is interpreted as representing a single storm event which transported siliciclastic debris into the shallow lagoon, mixing it with material from the adjacent shoreline and biostromal environments. This unit allowed many stromatoporoids to gain a purchase upon the substrate and its deposition heralded the development of the small patch-reef buildups in this area.

Two types of small-scale stromatoporoid-coral buildups are represented. Patch reefs (or "bommies") of columnar, bulbous or pillar shape resemble the "rauks" or sea-stacks of Riding (1981) diffuse patches of coverstone-framestone composed of low domical forms from which skeletal growth matched sedimentation rate. Sediment invagination at the margins of some of the bommie-type patch reefs likewise supports vertical accretion matching the rate of sediment deposition (Kershaw & Riding, 1978). Although the height of these structures is up to 1.5m, the growing surface may have been only a few tens of centimetres above the muddy sea floor.

Decreasing siliciclastic contribution to these units is a function of transgression, with the depositional environment being more distant from the shoreline up-sequence and change in nodular texture is controlled by the complimentary in-

crease in the carbonate components (Møller & Kvingan, 1988).

The average depth of modern, nearshore quiet, carbonate-dominant lagoons varies considerably and is typically 5-30m (Longman, 1981). Analogous inferred environments and facies with dendroid coralline wackestone, mudstone and floatstone from other sequences have been considered as much shallower (Read, 1973; Racki, 1993), as shallow as <1m when associated with intertidal and supratidal facies. Depths of up to 5m for the nodular limestone facies represents a maximum estimate of palaeodepth given proximity to shoreline; and depths of this lagoonal environment to which this facies relates were probably no deeper than this. There is no evidence of emergence.

PROXIMAL SHELF FACIES ASSOCIATION

Stromatoporoid biostromal facies (seven divisions) (Tables 5; 6)

Stromatoporoid-bearing biostromal units are subdivided into seven distinct facies representing the range of *in situ* stromatoporoid accumulations and their directly related sediments. These are:

- Stromatoporoid framestone
- Coverstone
- Micritic floatstone
- Silty rubbly floatstone
- Grainy floatstone
- Rudstone
- Associated packstone and wackestone

Distributions and thicknesses are variable for these often complexly interrelated minor facies and only notable occurrences are listed below.

STROMATOPOROID FRAMESTONE

FLETCHERVIEW: L779, BURDEKIN DOWNS: L781-2.

This facies forms a thick unit of massive to very crudely bedded stromatoporoid framestone (Fig. 3G,H) in which generally low domical and laminar stromatoporoids support a slightly to moderately impure packstone matrix. Smaller framebuilders are chaetetids, heliolitids and foliose alveolitids, mostly in growth position, but many are reoriented. Coarse matrix components are dominantly unabraded and include solitary rugose corals, *Stachyodes*, branching tabulates, molluscs, brachiopods and stromatoporoid fragments. Finer skeletal debris includes crinoid ossicles, mollusc hash and fragmented tabulates. Siliciclastics include fine clays, quartz grains

TABLE 4. Characteristics of inner shelf facies associations; nodular limestone facies. Letter in bold= *in situ*, italicised= fragmental and transported, plain text= reoriented or unabraded. R=rare, U=uncommon, C=common, A= abundant, D=dominant.

| INNER SHELF FACIES ASSOCIATION | | | | |
|---|--------------------------|----------------------|--------------------------------|--|
| Facies | Nodular limestone facies | | | |
| Lithology | mudstone | wackestone | patch bioherms | conglomerate |
| Fauna | | | | |
| Stromatoporoids | | | | |
| laminar | U | C | A | C |
| low-medium domical | U | C | D | C |
| high domical-bulbous | U | C | C | U |
| dendroid | U | C | C as a halo | U |
| Tabulate corals | | | | |
| ramose alveolitids | U | A | U | C |
| auloporids | U | C | U | U |
| <i>Heliolites</i> | U | A | U | C |
| domical alveolitids | | C | U | C |
| foliose alveolitids | | C | R | U |
| Rugose corals | | | | |
| solitary (small) | U | A | | C |
| solitary (long/delicate) | | C | | C |
| Chaetetids | U | C | R | C |
| Bivalves | U | A | R in matrix | U |
| Nautiloids | U | C | | |
| Gastropods | | U | | |
| Crinoids | | U | | |
| Brachiopods | U | U | R in matrix | U |
| Bedding features | | | | |
| massive (M), very thick (v), thick(T), medium (m), thin (h) | T | T | n.a. | T |
| planar lamination | | | | minor |
| Nodules | D | D | | |
| Stylolites | | | | |
| sharp high amplitude | U | U | U | |
| low sinuosity | D | D | | |
| Grain sizes | | | | |
| clastics | clay-silt | clay-vfsand | | to cobble |
| carbonates | mud dominant + fauna | mud dominant + fauna | | |
| Bioturbation | extensive | extensive | | |
| Clastic grain types | clay, qtz, bio | | | qtz, felds, biot, clay, micritic intraclasts, granodiorite |
| Impurity | <5% | <5% | | to 60% |
| Carbonate fabric | mudstone | wackestone | localised framestone bindstone | |

ranging from silt to fine sand, and biotite flakes to medium sand size. Reef-top energy was sufficient to reorient some framebuilders.

DISCUSSION

Stromatoporoid framestone is indicative of *in situ* reefal development (Longman, 1981; James 1983). Lateral facies relationships shows that such reefs were of low relief, standing no more than a few metres above the surrounding sea-floor and were locally extensive. The margins of such bioherms were gently sloping rather than steep sided. Broad inter-reef debris channels developed between the bioherms. Reorientation of some larger framebuilders suggest storm or wave turbulence on the reef top (Read, 1973; James, 1983) but the matrix lithology reflects the rather subdued prevailing conditions and many inter-frame shelters. Recesses were occupied by a number of dendroid and fasciculate taxa including *Stachyodes*, *Sociophyllum* sp. (Zhen, 1991), and alveolitids all rarely preserved in growth position. The preponderance of laminar and low domical stromatoporoid growth forms reflects high energy, hard substrate, encrusting associations in well circulated, well lit, extremely shallow, turbulent water (Lecompte, 1970; Riding, 1981; James, 1983; Kano, 1990). Water depths for the reef were shallow, less than 10m depth (turbulent zone of Lecompte, 1970; Embry & Klovan, 1971), and may have been as shallow as 2-3m (Read, 1973). There is no evidence for emergence.

Siliciclastic components indicate proximity to the shoreline and a terrigenous source. The bioherms were within a few kilometres of shore and can be regarded as fringing reefs (*sensu* Johnson & Carter, 1987; Johnson & Risk, 1987).

COVERSTONE

FLETCHERVIEW: L779, BURDEKIN DOWNS: L781, FANNING RIVER CAVES: L803, HORSESHOE BEND: L787.

Coverstone facies include both laminar stromatoporoid coverstone and foliose alveolitid coverstone. Stromatoporoid coverstone is medium to thickly bedded and consists of large, up to 1.7m wide, laminar stromatoporoids supporting a moderately impure silty wackestone matrix containing dispersed tabulate and rugose corals, molluscs and rare brachiopods. This facies occurs as interbeds with wackestone and packstone (described below) in particular at the base of the major framestone unit at Fletcherview (L779), Burdekin Downs (L781) and also within Fanning River Caves L803 (Figs 3G, 4A). At L787, a thin

<2m, restricted unit of foliose alveolitid coverstone with a slightly impure wackestone matrix is interbedded with coralline wackestone and packstone.

DISCUSSION

These units are interpreted as representing sheltered lagoonal deposition in which laminar stromatoporoids grew rapidly laterally in order to gain a purchase upon the muddy substrate (James, 1984). Immediate vertical passage to framestone suggests lagoon floor laminar stromatoporoid pavements that were a pre-reefal, initial stage of reef growth upon a muddy proximal shelf, in water depths less than 5m, or an intra-biostromal lagoonal phase in equally shallow water. Stromatoporoid coverstones thus represent the near-reef development of short lived stromatoporoid communities in a nearshore or proximal shelf environment. Intercalation with packstone and wackestone suggest periodic reworking of bioclastic debris across such communities, but fine grained interstitial lithologies suggest generally quiet lagoonal conditions. Tabulate coral coverstones are relatively pure, medium bedded and locally restricted, and represent very localised tabulate pavement development within the inshore environment of carbonate dominance.

MICRITIC STROMATOPOROID FLOATSTONE

FANNING RIVER: L788, FANNING RIVER NORTH: L789, FANNING RIVER CAVES: L791, KIRKLAND DOWNS: L798, CALCIUM AREA (cf Wyatt et al., 1970: 24).

The facies is characterised by locally extensive, thickly to very thickly bedded floatstone in which dispersed large, low to high domical stromatoporoids which are enclosed in a coral-mollusc-brachiopod wackestone. The facies is interbedded and interdigitated with rubbly floatstone, rudstone and dendroid coral packstone. Faunal elements include stromatoporoids, smaller heliolitid colonies, rare chaetetids and very commonly the large brachiopod *Stringocephalus*. Smaller fossils include dendroid stromatoporoids, particularly *Amphipora ramosa*, branching tabulates and solitary rugose corals, and smaller brachiopods and molluscs. Colonial rugose corals are common in this facies at Kirkland Downs. The matrix is extensively bioturbated, dark and fine grained. Siliciclastic components are generally of low abundance, but lower units in the Fanning River area are moderately impure containing silt and rarer sand sized material. Most skeletal components are simply toppled and show little sign of transport or abra-

TABLE 5. Characteristics of proximal shelf facies association; Biostromal facies continues Table 6. Letter in bold= *in situ*, italicised= fragmental and transported, plain text= reoriented or unabraded. U= uncommon, C= common, A= abundant, D=dominant. 1 Alveolite coverstone is a variant of this facies.

| PROXIMAL SHELF FACIES ASSOCIATION | | | | | | |
|--|--|------------|----------------------|-----------------|------------------------------------|--------------------|
| Facies | Biostromal facies | | | | | |
| Lithology | Stromatoporoid framestone | | Coverstone | Rudstone | Micritic stromatoporoid floatstone | Grainy floatstone |
| Fauna | frame | matrix | | | | |
| Stromatoporoids | | | | | | |
| laminar | A A | A | D A | | C C C | C C C |
| low-medium domical | D D | A | A | C | C A C | A A C |
| high domical-bulbous | C C | C | | C | C A C | A C C |
| dendroid | | U C | C | C | R A C | A A - D |
| Tabulate corals | | | | | | |
| ramose alveolitids | | C C | C | C | C C | U C |
| auporids | | U | | | | |
| <i>Heliolites</i> | C C | C | C | C | C C | C C C |
| domical alveolitids | C C | C | | C | C | C C |
| foliose alveolitids | | C C | D * 1 | | C | U? C |
| Rugose corals | | | | | | |
| solitary (small) | | C C | C | C C | A | C C |
| colonial | | | | | Kirkland Downs area | |
| solitary (long/delicate) | | C C | | | A | U |
| Chaetetids | C C | C C | U | U | A | U C C |
| Bivalves | | C | U | U | C A | U |
| Nautiloids | | U | | | U | R |
| Gastropods | | U | U | R | U | U |
| Crinoids | | C | C | C | U | C |
| Brachiopods | | | | | | |
| <i>Stringocephalus</i> sp. | | | | C C | A A A | |
| atrypids | | C C | C | R | A A A | |
| other | | C C | C | U | A A A | U U |
| Bedding features | | | | | | |
| massive (M), very thick (V), thick (T) | M | | T - h | M, V - T | V - T | M - T |
| Bedding features | Sporadic lamination in mtx very crude bedding lamination in framestone fabric | | crude imbrication | | | weak cross laminae |
| Nodules | C | | | | C | U |
| Stylolites | | | | | | |
| sharp high amplitude | C | | | C | | C |
| low sinuosity | A | | C | | C | C |
| Grain sizes | | | | | | |
| clastics | clay-med sand | | silt-vfsand | silt-vfsand | clays | med-coarse sand |
| carbonates | mud boulder | | mud-cobble | to boulder | | |
| Bioturbation | extensive in mtx | | extensive | | extensive | |
| Clastic grain types | clay, qtz, biotites | | clay, qtz | qtz?, clays | clay | qtz?, clay biotite |
| Impurity | 2-35% | | | 2-20% | < 5% | < 5% |

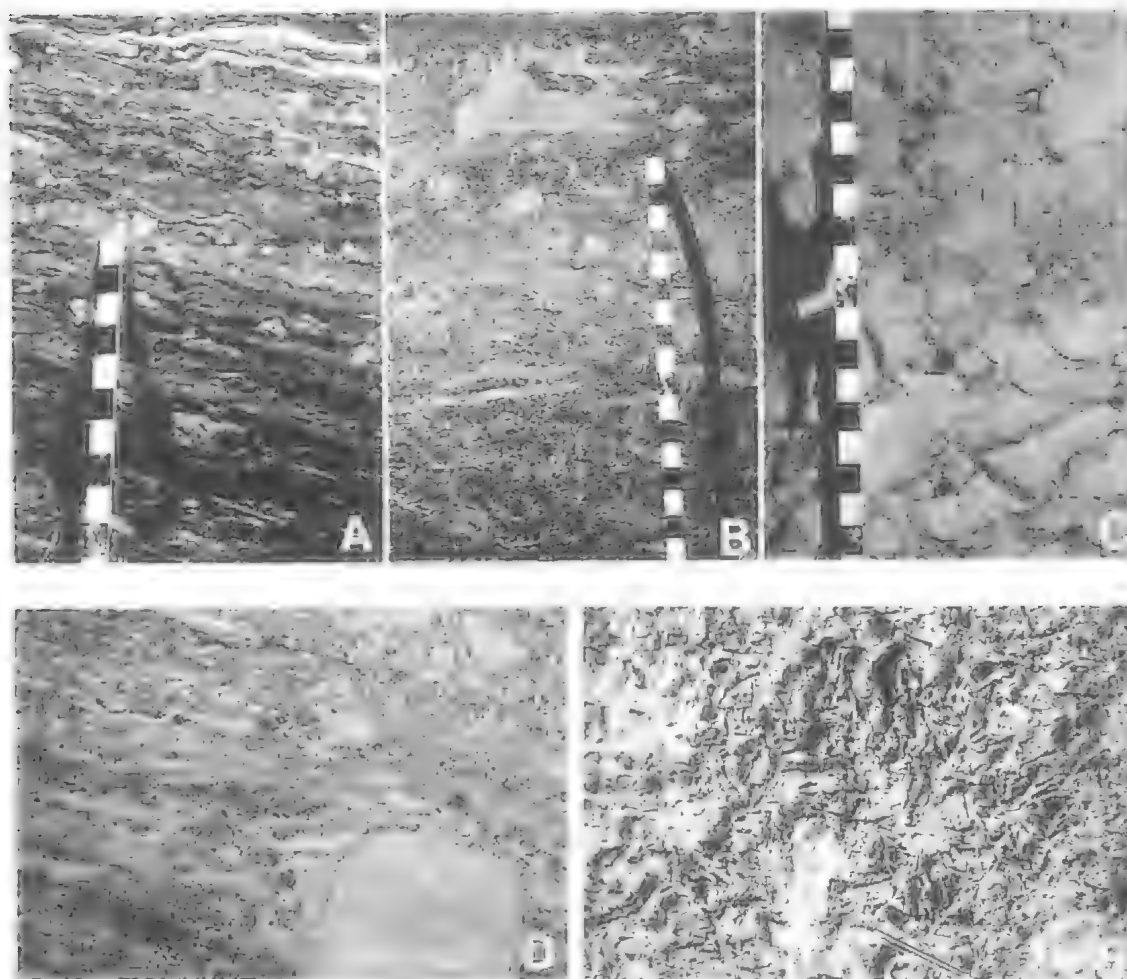


FIG. 4. A, coverstone units interbedded with highly impure packstones and wackestones. B, grainy floatstone. C, massive rudstone unit. D, silty rubbly floatstone facies. All from Maternity Cave, Fanning River Caves L803. E, "Spaghetti stone" fasciculate coral packstone of the coralline packstone facies, Fletcherview L779.

sion. Larger skeletons are *in situ* but some are reoriented. A variant of this facies is represented by beds with an abundance of *Stringocephalus* sp. in the vicinity of Fanning River (L788) and Fanning River North (L789) where large *terebratulids* and *stromatoporoids* form a brachiopod-stromatoporoid biostromal unit interbedded and interdigitated with brachiopodal rudstones.

DISCUSSION

The dominance of muddy matrix, delicately dendroid forms and only limited reorientation of larger skeletons suggest quiet water, restricted, shallow conditions. Absence of significant siliciclastics in most occurrences suggests terrig-

enous input was diminished by distance from shoreline, and/or more proximal biostromes acting as a buffer to siliciclastics thus restricting the terrigenous supply to biostromal zones further offshore. The succession of some biostrome sequences by impure limestone-sandstone association suggests that their development was close enough to shore to be terminated by major clastic pulses.

Extensive *Stringocephalus*-stromatoporoid biostromes are common features in Middle Devonian sequences. Krebs (1974), Burchette (1981), and Racki (1993) regarded them as laterally extensive, sheet-like bodies deposited in lagoonal environments. Substantial accumulations of this brachiopod within a diverse assemblage

suggests generally calm lagoonal to peribiotromal deposits (Racki, 1986; 1993). Reorientation of larger skeletons and dendroid toppling suggests some episodic turbulent reworking, whereas intercalation and interdigitation with rubbly floatstone and rudstone indicates local high energy reworking (Racki, 1993; Read, 1973). Water depths were in the order of 1-13m (Read, 1973).

Thus the facies is interpreted as a series of extensive biostromal stromatoporoid pavements interspersed with dendroid coralline-*Amphipora* thickets, in a shallow, quiet water, carbonate-dominant environment.

SILTY RUBBLY FLOATSTONE

FANNING RIVER: L788 and adjacent section. FANNING RIVER NORTH: L789. FANNING RIVER CAVES: L791, L803.

Laterally discontinuous, thick bedded and commonly crudely laminated floatstone contains dispersed stromatoporoid skeletons (Fig. 4D), both *in* and *ex situ*, supported by a moderately to highly impure carbonate matrix containing short tabulate coral sticks, solitary rugose corals and fragmental stromatoporoid, molluscan, and coralline debris. The fine matrix consists of sandy silt and fine skeletal debris such as mollusc hash, crinoid ossicles and coral fragments. A striking feature of the facies is the abundant bioclastic debris. Interbeds with less abraded, coral-rich units, containing branching and more delicate forms are also common.

DISCUSSION

Silty rubbly floatstone represents dispersed stromatoporoid coral biostromes, similar in character to the biostromal pavements discussed above, which were reworked by episodic storm events. Elevated siliciclastic content, and lateral and vertical relationships to siliciclastic facies and basement, suggest a location close to the shoreline. The facies typically overlies either a muddy unit or rudstone. It is intimately associated with micritic floatstone and thus represents moderate energy, stromatoporoid biostromes that were developed at shallow water depths (Leavitt, 1968; Noble, 1970; Read, 1973; Racki, 1993).

GRAINY FLOATSTONE

FLETCHERVIEW: L780, L778.

The facies consists of extremely thick bedded, massive, or very crudely bedded, massive or very crudely laminated stromatoporoid floatstone, possessing large overturned and *in situ* domical stromatoporoids, heliolitids and rare chaetetids

set in a supporting matrix of coarse coralline and stromatoporoid debris (Fig. 4B). Coral and stromatoporoid debris range from coarse sand to cobble size and includes fragmented large stromatoporoid bioclasts, common broken sticks of *Amphipora* and tabulate corals and accessory crinoid ossicles.

DISCUSSION

Lateral passage to framestone suggests that this facies represents high energy channels or sheets of debris adjacent to, and between, low relief biohermal buildups. In this sense it can be regarded as representing intra-bioherm reef flats (Longman, 1981). Dendroid *Amphipora* and large stromatoporoids are *in situ* or were derived from subjacent bioherms or *Amphipora* thickets (Tsien, 1981). Fines were winnowed out by wave or current action (Leavitt, 1968; Longman, 1981). These deposits must have been, in part, storm generated in the shallow proximal shelf between and adjacent to bioherms. Water depths were possibly up to 3m (Wilson, 1974), consistent with the low relief inferred for local bioherms. Crude lamination and bedding suggesting depths of 1 to 3m (Read, 1973; Wilson, 1974).

RUDSTONE

FANNING RIVER: L788. FANNING RIVER NORTH: L789. FANNING RIVER CAVES: L791, L803.

Various clast supported stromatoporoid conglomerates are grouped into this facies. Such rudstones thick to very thickly bedded and crudely laminated. They are highly variable, ranging from pebbly stromatoporoid bioclast conglomerates to stromatoporoid boulder conglomerates. Fining upwards to rubbly floatstones is common. Grain size is trimodal with large stromatoporoid bioclasts, smaller coral bioclasts and finer subordinate carbonate bioclasts and, more commonly in lower parts of the sequence, siliciclastic silt and sand. Larger clasts display poorly developed imbrication.

DISCUSSION

Thickest units, such as those exposed within Fanning River Caves (Fig. 4C) may represent reef flank debris deposits (Wilson, 1974; Playford, 1980; James, 1983), but thick bedded units laterally and vertically associated with micritic floatstones represent local reworking of near *in situ* bioclasts by high energy episodes (Leavitt, 1968).

ASSOCIATED PACKSTONE AND WACKESTONE
FANNING RIVER: L788, FANNING RIVER NORTH: L789.
FANNING RIVER CAVES: L791, L803. KIRKLAND
DOWNS: L798.

This heterolithic facies groups interbedded packstone and wackestone units found in association with other biostromal facies. Medium to thick bedded, ubiquitously bioturbated, packstone and wackestone contains abundant coralline, stromatoporoid and shelly debris within a pure to moderately impure matrix. Units are locally restricted and laterally grade into related biostromal facies. Their textural characteristics reflect the associated biostromal facies: dark micritic wackestone with a branching coral-stromatoporoid biota are associated with micritic stromatoporoid biostromes whereas moderately impure silty packstones are associated with silty, rubbly floatstones.

DISCUSSION

Deposition took place laterally from biostromal units, representing intra- and inter-biostromal sediments accumulated by current activity, where slight variations in depth, wave energy and circulation periodically prohibited biostromal development. Depositional depths were similar to that of the micritic stromatoporoid floatstone.

SUMMARY

The biostromal association represents variable development of reefoid deposits: stromatoporoid biostromes, low bioherms, pavements and their associated sediments, within a variety of proximal shelf environments ranging from very nearshore banks to offshore carbonate shelf.

Siliciclastic impurities within facies and siliciclastic pulses between facies packages confirm that many of these reefoid communities were proximal to the shoreline and were thus "fringing" in the modern sense of fringing reefs (James, 1983; Johnson & Risk, 1987; Johnson & Carter, 1987). Two fundamental styles developed:

(1) In the Fletcherview-Burdekin Downs area the main reefoid phase is the coverstone-framestone-grainy floatstone assemblage which represented a low relief bioherm, with leeward flanking stromatoporoid pavement upon a muddy substrate and inter/intra biohermal channelised coarse skeletal floatstone accumulations.

(2) In the Fanning River Area, and subordinated elsewhere (Kirkland Downs, Calcium see Wyatt et al. 1970, and other basin margins) extensive biostromal stromatoporoid-coral-brachiopod biostromes developed across much of the proximal shelf, extending very close to the shore-

line. Unit outcrop and local variation suggests that individual stromatoporoid biostromes were wide and laterally extensive over several hundreds of metres to kilometres, but were patchy, contained large zones of storm worked rubble, and quieter slightly deeper, large stromatoporoid-poor areas. Some channels or localised erosional slopes of coarser rudstone developed throughout the bank complex.

Dispersed stromatoporoid packstone facies (Table 6)

DIAGNOSIS

Thick-bedded, fasciculate coral packstone with dispersed laminar stromatoporoids.

DISTRIBUTION

HORSESHOE BEND: L787. BIG BEND: L792,
FLETCHERVIEW: L806.

DESCRIPTION

Whereas this association could be placed within the biostromal group of facies it is sufficiently distinct to warrant separation. Thick bedded coralline packstone, with abundant fasciculate corals contains very common, but widely dispersed, laminar to low domical stromatoporoid skeletons up to 0.8m wide, scattered heliolitids and foliose or reptant tabulate corals within a muddy matrix.

DISCUSSION

Deposition appears to have been restricted to offshore, shallow, quiet water seaward of major stromatoporoid bank development or adjacent to it. The facies is interpreted as a transition between true stromatoporoid pavements and offshore coralline thickets. Water depths probably were near the lower limit of biostromal deposition, approaching 5-10m (cf. Read, 1973; Playford, 1980), ranging into slightly deeper water above normal storm wave base (5-20m) (Klovan, 1974; Read, 1973; Racki, 1993). Skeletal debris production can be attributed to storm wave reworking, but in general larger skeletal structures are undisturbed.

Endophyllum siltstone facies (Table 6)

DIAGNOSIS

Patch reefs of colonial rugose corals, heliolitids and rare stromatoporoids enclosed within calcareous siltstones, containing a rich coral-brachio-

TABLE 6. Characteristics of proximal shelf facies association; Biostromal facies continued, dispersed stromatoporoid packstone and *Endophyllum* siltstone facies. Letter in bold= *in situ*, italicised= fragmental and transported, plain text= reoriented or unabraded. U= uncommon, C= common, A= abundant.

| PROXIMAL SHELF FACIES ASSOCIATION | | | | |
|--|--|-------------------------------------|------------------------------------|------------------------------|
| Facies | Biostromal facies | | Dispersed stromatoporoid packstone | <i>Endophyllum</i> siltstone |
| Lithology | Silty rubbly floatstones | Associated packstone and wackestone | | |
| Fauna | | | | |
| Stromatoporoids | | | | |
| laminar | C A | C | A U | U |
| low-medium domical | A A | C | C U | U |
| high domical-bulbous | A A | C | | C |
| dendroid | C A | C | C - A C | U |
| Tabulate corals | | | | |
| ramose alveolitids | C A | C C | C C | A |
| auloporids | A *1 | U U | C | A |
| <i>Heliolites</i> | A | U C | C | C A |
| domical alveolitids | C | U C | C | C A |
| foliose alveolitids | C | C C | C | C |
| Rugose corals | | | | |
| solitary (small) | C C | C | C C | C |
| colonial | | | | A |
| solitary (long/delicate) | C C | C | C | C |
| Chaetetids | C C C | C C | U | C |
| Bivalves | C | C | C | C |
| Nautiloids | U | C | C | U |
| Gastropods | U | C | C | U |
| Crinoids | U | C | C | |
| Brachiopods | | | | |
| <i>Stringocephalus</i> sp. | C C | C C | | U |
| atrypids | | | | A |
| other | C C | C C | C | A |
| Bedding features | | | | |
| massive (M), very thick (V), thick (T) | M | V - M | V - T | T - M |
| planar lamination | SOME CRUDE | | | C |
| Nodules | U | C | U | C |
| Stylolites | | | | |
| sharp high amplitude | C | C | | |
| low sinuosity | A | A | | |
| Grain sizes | | | | |
| clastics | silt coarse sand | silt-coarse sand | clays | silt-vfsand |
| carbonates | to boulder | to cobble | | |
| Bioturbation | pervasive, extensive | pervasive, extensive | extensive | extensive |
| Clastic grain types | qtz, clays, felds, rare granitoids, biot | biot, qtz, clays | clays | qtz, clays |
| Impurity | <35% mostly 10-15% | highly variable | <2% | up to 50% |
| Carbonate fabric | floatstone-rudstone | packstone-wackestone | packstone-floatstone | siltstone, patchy framestone |

1 common as encrustors

pod assemblage, in the uppermost Burdekin Formation.

DISTRIBUTION

FANNING RIVER CAVES: L791. FANNING RIVER: L788

DESCRIPTION

This facies is the uppermost expression of the Burdekin Formation in the Fanning River area representing a transition to the Cultivation Gully Formation. It becomes increasingly silty (siliciclastic-dominated) up-section where it is characterised by medium bedded, moderately to highly impure, silty, wackestone which grades to variably bioturbated fossiliferous siltstone enclosing isolated colonies or aggregations of *Endophyllum columna columna* up to 1.2m wide. Associated with the *Endophyllum* aggregations are *Heliolites* sp., laminar encrusting stromatoporoids, atrypid brachiopods, laminar and dendroid tabulate corals, solitary rugose corals and rare large sponge colonies. This facies extends, as lenticular bodies into the basal Cultivation Gully Formation.

DISCUSSION

The facies represents quiet water, exclusively subtidal deposition under increasing siliciclastic input where isolated coral colonies and small microatolls developed on the muddy offshore substrate. A shallow (ca. 20m) water depositional environment above wave base is envisaged for this facies, probably at slightly greater depths than other biostromal units. Minor reorientation and abrasion of coralline and other debris attests to some periodic wave energy, against a background of dominant low energy conditions. The development of coralline microatolls, only 1-2m in size, with subordinate stromatoporoids may be a function of regression and higher clastic input, a slightly deeper water biotope (Lecompte, 1970; Playford, 1980), or better ability of coralline forms to eject clastic particles.

DISTAL SHELF ASSOCIATION

Coralline packstone facies (Table 7)

DIAGNOSIS

A diverse assemblage of fasciculate coral and *Amphipora* packstone and mixed skeletal packstone, ranging from relatively pure to moderately impure, containing dispersed, mostly

domical, stromatoporoids, heliolitids and delicate auloporids or tabulate coral debris.

DISTRIBUTION AND THICKNESS

Most sections major occurrences are :
FLETCHERVIEW: L778; 18m. L779; 38m. L780; 30m.
BURDEKIN DOWNS: L781-2; 16m. FANNING RIVER: L788; 52m. FANNING RIVER CAVES: L791; two units 80m, 40m. FANNING RIVER NORTH: L789; 30m approximately. GOLDEN VALLEY: L800 15m approximately. HORSESHOE BEND: L787; four main units, 20-30m thick. Kirkland Downs: L796; 11m approximately.

DESCRIPTION

This portmanteau association is a diverse assemblage of relatively pure skeletal packstone and subordinate wackestone ranging from fasciculate coral packstone, *Amphipora* packstone to mixed skeletal debris packstone. The association is locally and regionally variable but in general is thick bedded, bioturbated and contains a diverse coral, brachiopod, and subordinate stromatoporoid fauna. Coralline packstone varies from abraded skeletal packstone to fasciculate coral packstone dominated by toppled and non-abraded faunas (Fig. 4E). *Amphipora*-coral packstones, often moderately impure, contain abundant *Amphipora pervesiculata* and thin *Cladopora* sp. Coralline packstones commonly contain dispersed stromatoporoid, heliolitid and delicate aulopodid skeletons. The association is transitional to crinoidal grainstone in the Fletcherview area, but in the type section non-abraded coralline packstone containing abundant brachiopods (especially atrypids) is transitionally replaced by *Endophyllum* siltstone.

DISCUSSION

Deposition of this facies took place seaward of biostromal and biohermal development in open shelf, shallow water. Storm and current reworking of material on the shallow shelf produced abraded deposits, but quiet water, sheltered conditions predominated and resulted in widespread development of fasciculate coral thickets, *Amphipora* thickets and a range of faunally diverse communities. *Amphipora* thickets developed in depths as shallow as 1m (Read, 1973) but lateral relationships, preservation of branched forms and the increasing dominance of tabulate corals suggest a depositional depth near the lower limit of biostrome formation, approaching 20m (Lecompte, 1970; Klován, 1974; Racki, 1993). Tabulate coral-rich packstone probably represents deeper, well circulated depositional envi-

TABLE 7. Characteristics of the distal shelf facies association. Letter in bold=*in situ*, italicised= fragmental and transported, plain text= reoriented or unabraded. R= rare, U= uncommon, C= common, A= abundant, D=dominant. 1. mostly in bioherms

| DISTAL SHELF FACIES ASSOCIATION | | | | | |
|--|--|----------------------|-------------------|--------------------------|--------------------|
| Facies | Crinoidal grainstone | Coralline packstone | | | Micritic carbonate |
| Lithology | | Amphipora packstones | "Spaghetti stone" | tabulate-coral packstone | |
| Fauna | | | | | |
| Stromatoporoids | | | | | |
| laminar | R R C | R U | R U | R U *1 | |
| low-medium domical | R R C | R U | | R U *1 | |
| high domical-bulbous | R R C | R R U | | C R U *1 | |
| dendroid | U | A - D A | | A - D *1 | |
| Tabulate corals | | | | | |
| ramose alveolitids | C | A | A | A C C | R R |
| auloporids | | | A | A C C | |
| <i>Heliolites</i> | C C | A | A | A C | |
| domicile alveolitids | C C | | C | C C C | |
| foliose alveolitids | C | | C | C C C | R R |
| Rugose corals | | | | | |
| solitary (small) | C | C | A | A | R |
| colonial | | | | | |
| solitary (long/delicate) | C | C | A | A | |
| Chaetetids | R R U | U | U | U | |
| Bivalves | C | C | C | C | |
| Nautiloids | | U | U | U | R |
| Gastropods | C | | | | |
| Crinoids | A - D | C | C | C | |
| Brachiopods | | | | | |
| <i>Stringocephalus</i> sp. | | | | | |
| atrypids | | | | | R |
| other | C | C C | C C | C C | |
| Bedding features | | | | | |
| massive (M), very thick (V), thick (T) | M | V - M | V - T | | T - M |
| planar lamination | SOME CRUDE | | | | C |
| Nodules | U | C | U | | C |
| Stylolites | | | | | |
| sharp high amplitude | C | C | | | |
| low sinuosity | A | A | | | |
| Grain sizes | | | | | |
| clastics | silt-coarse sand | silt-coarse sand | clays | | silt-vfsand |
| carbonates | to boulder | to cobble | | | |
| Bioturbation | pervasive, extensive | pervasive, extensive | extensive | | extensive |
| Clastic grain types | qtz, clays, fspar, rare granitoids, biot | biot, qtz, clays | clays | | qtz, clays |
| Impurity | < 35% mostly 10-15% | highly variable | < 2% | | up to 50% |

ronments possibly as deep as 25-30m (Klovan, 1974; Playford, 1980).

Crinoidal grainstone facies (Table 7)

DIAGNOSIS

Thick-bedded, skeletal grainstone containing abundant, sand-sized coral and crinoidal debris that is commonly planar laminated or rarely cross-laminated.

DISTRIBUTION AND THICKNESS

FLETCHERVIEW: L778; approximately 5m. BURDEKIN DOWNS: L781; approximately 4m.

DESCRIPTION

Thick bedded crinoidal grainstones show prominent but restricted development in the vicinity of Fletcherview-Burdekin Downs where they are transitional from coralline packstone and form the uppermost well exposed units of the Burdekin Formation in that area. Grainstones are thickly to very thickly bedded, sporadically cross bedded, weakly laminated and sporadically cross-laminated, and contain moderately well-sorted, granule sized skeletal debris including crinoid ossicles, commonly with micrite rims, and rare ooids. Larger tabulate corals and stromatoporoids are present, but are mostly *ex situ*. Siliciclastic components are restricted to uncommon, fine, quartz grains.

DISCUSSION

Deposition took place within a well circulated, shallow environment, removed from clastic input where tidal and other currents produced carbonate sand dune bedforms (Ball, 1967; Enos, 1983; Bjerstedt & Feldmann, 1985). Water depths may have been as shallow as 3-5m (Ball, 1967). Given the estimated depths for the underlying coralline packstone, and the sporadic presence of large stromatoporoids, a range of <20m is estimated (cf. Embry & Klovan, 1971; Klovan, 1974). As for the coralline packstone facies, leeward bioherms restricted siliciclastic input to this facies. There is no positive evidence for emergent shoaling.

Micritic carbonate facies (Table 7)

DIAGNOSIS

Poorly represented, thick-bedded dark carbonate mudstone with rare wackestone patches.

DISTRIBUTION

GOLDEN VALLEY: thickness indeterminate, greater than 100m.

DESCRIPTION

This facies is developed to the SW of Golden Valley, where it is at least 100m thick overlying the coralline packstone facies. Local folding and faulting prevents accurate assessment of the thickness. Monotonous, medium bedded, dark grey, micritic carbonate mudstones enclose rare patches of coralline and brachiopod wackestone. Macrofauna is sparse and includes rare nautiloids, very rare tabulate corals, rare solitary rugose corals and uncommon atrypid brachiopods. Bioturbation is common throughout. Minor silicification is evident but detrital clastic impurities so common in other facies are absent.

DISCUSSION

The fine grained, micritic texture and the paucity of shallow water benthos suggests this facies represents quiet "deeper" water shelf deposition in comparison to other associations of the Burdekin Formation. Deposition occurred beneath wave base and the presence of a sparse benthos suggests that deposition was at the local limits of coralline development in low circulation, low light conditions. Estimates for depth are between 25-80m (see Playford, 1980; Noble, 1970; Embry & Klovan, 1971). Given the small scale of the Burdekin carbonate system, a shallower, rather than deeper deposition within this range is suggested.

RELATIONSHIPS

Facies and facies association relationships are highly complex within the Big Bend Arkose and Burdekin Formation. Although a general successional trend is apparent, local facies mosaics are complex and reflect local nuances in basement topography, biostromal and biohermal architecture, source of siliciclastic input, and other local palaeogeographic conditions. Lateral facies variations indicate spatial relationships between environments across the shallow shelf. A discussion of these trends is presented in terms of individual areas: Fletcherview-Burdekin Downs, Fanning River Caves-Fanning River-Fanning River North, Horseshoe Bend-Golden Valley, and other scattered areas.

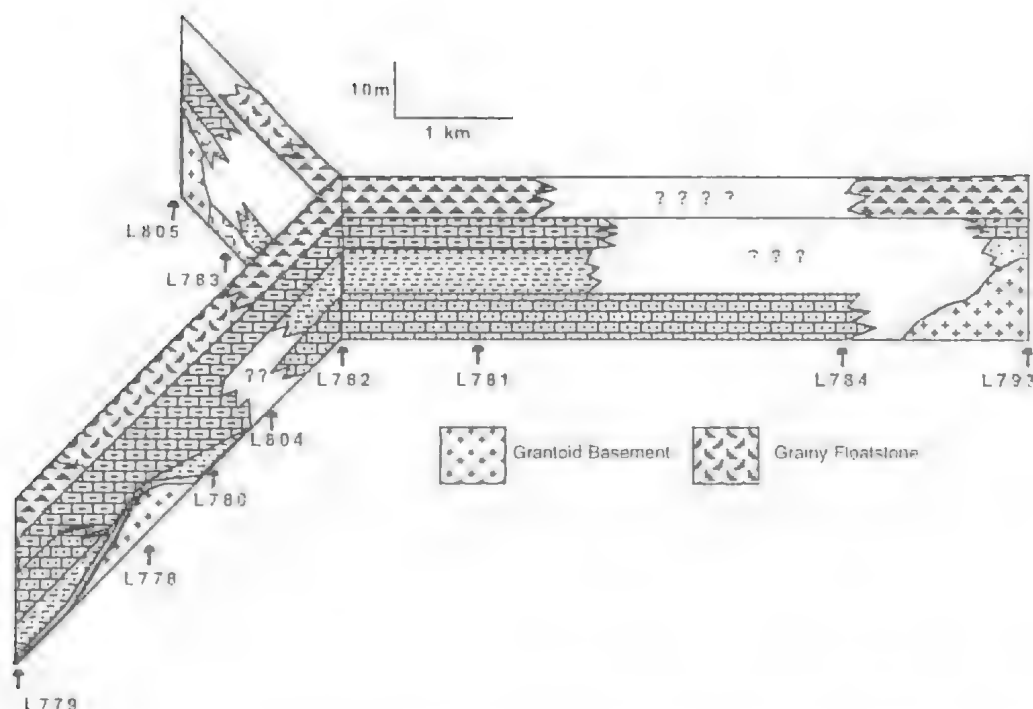


FIG. 5. Interpreted inner and proximal shelf facies mosaic of the Fletcherview-Burdekin Downs area. Legend as for Fig. 2 except as indicated. Scale approximate.

FLETCHERVIEW-BURDEKIN DOWNS AREA

INNER SHELF ASSOCIATION

Almost all basal units are marine with non-marine facies present at only one locality (L783). Boulder conglomerates at L805, L793 and L780 suggest headlands at these sites. Sandy siliciclastics are poorly represented within basal units; the area was dominated by low energy inshore depositional environments. Transition to carbonate-dominated environments was generally rapid; but fluvial outfall near L779 resulted in deposition of impure limestone-sandstone facies. Growth of small stromatoporoid bommies (patch reefs or "rauks") in the proximal carbonate muddy lagoon was widespread, a prelude to the main biohermal phase in this area. Thicknesses of inshore associations are greatest at L781 and L779. All thicknesses suggest that the inshore "lagoonal" deposition was of limited extent in time and space, with reefal development less than a few kilometres offshore. Lateral relationships (Fig. 5) suggest that L778 was locally high, L779 more proximal to river outfall, and lagoonal sediments

at L778 generally removed from siliciclastic input.

PROXIMAL SHELF ASSOCIATION

Stromatoporoid framestone at L779, and as seen in the continuous outcrop between L781 and L782, dominates the proximal shelf facies in this area. These framestones transitionally overly patchy coverstones which suggest a back reef gradient from laminar stromatoporoid lagoon to bioherm proper which was laterally extensive along and across the shelf floor. Lateral passage to grainy floatstones at L778 and L780, and patchy stromatoporoid framestone at L806, suggests a reefal mosaic (Fig. 5). Biohermal growth in the vicinity of L779 was terminated by a siliciclastic pulse, now represented as impure (biotite-rich) *Amphipora* and coralline packstones. This further indicates the proximity to terrigenous sediment supply of this locality. Detrital influx was a short-lived episode, followed by coralline packstone indicating the development of coralline thickets. Biohermal development subsequently waned in the Burdekin Downs area (L781-2), and replaced by coralline packstone

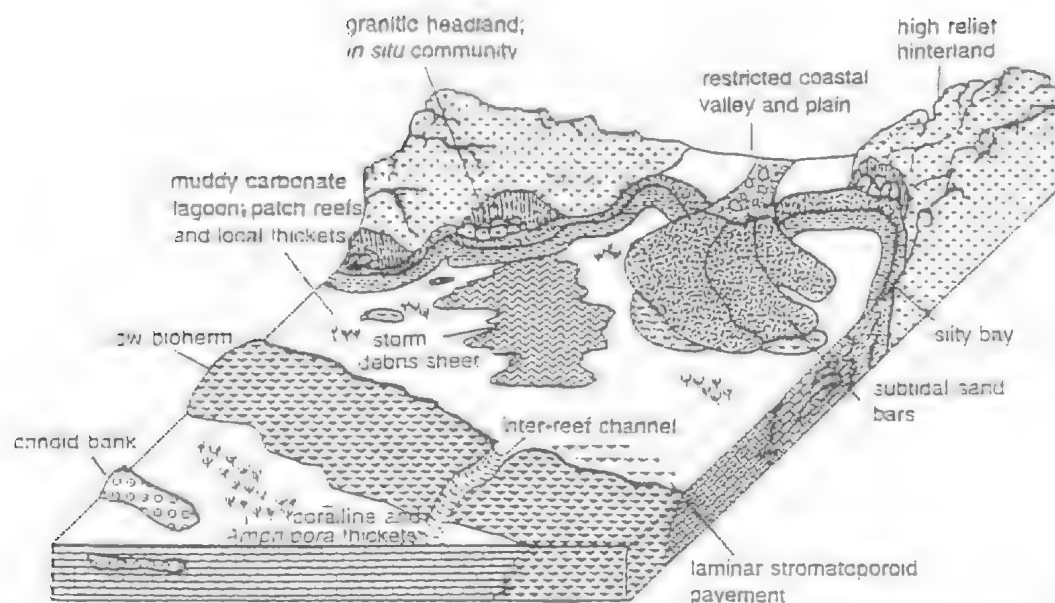


FIG. 6. Reconstructed palaeogeographic and depositional setting for the Fletcherview-Burdekin Downs area.

representing tabulate coral-*Amphipora* thickets. Adjacent higher energy facies were also succeeded by coralline packstone marking the gradual transition to distal shelf facies.

DISTAL SHELF ASSOCIATION

Thick successions of coralline packstone are best interpreted to represent a wide, shallow, stable, distal carbonate shelf, seemingly extensive across the majority of the area. Individual successions of coralline packstones are locally variable, especially in the units immediately above the biostromal facies. At both Burdekin Downs (L781-2) and Fletcherview (L779) the succession is from *Amphipora*-rich thickets to more tabulate coral-rich units. Scattered stromatoporoid colonies and groups of colonies suggest the fore-reef zone was patchily developed. Sporadic occurrences of larger stromatoporoids throughout highlight the shallow nature of the distal shelf. At Burdekin Downs (L781), delicate tabulate coral and heliolitid communities are interspersed with *Amphipora* thickets. Spectacular occurrences of rugose coral-tabulate coral-*Amphipora* rich facies or "spaghetti stone" at Fletcherview (L779) show major development of delicate coral-stromatoporoid thickets in the fore-reef shelf. Crinoidal-rich grainstones in this area show development of some mobile carbonate sand bodies on the distal shelf floor.

A reconstructed palaeogeography for the Fletcherview area is presented in Fig. 6. It depicts a thin inner shelf, wide biostromal zone and extensive carbonate distal shelf. This area lacks thick siliciclastic development, is dominated by facies of quiet water aspect and has true reefal development.

BIG BEND

Outcrops at Big Bend have been studied by a number of authors (Heidecker, 1959; Lang et al., 1990; Zhen, 1991). Re-examination of this site revealed an abundance of marine siliciclastic units, a thin interval of inner shelf facies, and substantial development of the proximal shelf, dispersed stromatoporoid packstone facies. Distal shelf coralline packstone marks the upper part of the succession.

An abundance of inner shelf siliciclastics contrasts sharply with the sequence displayed at Fletcherview, reflecting the localised occurrence of such facies. Thin, mixed facies elements such as fossiliferous siltstone and inner shelf impure nodular limestone suggests that the siliciclastic to carbonate transition was abrupt. Extensive biostromes did not develop in this immediate area. Rather, dispersed stromatoporoid packstone represents the lateral equivalent of reefal facies developed at Fletcherview and Burdekin Downs.

Coralline packstone is the only manifestation of the distal shelf association. Thus this area is interpreted as having been proximal to terrigenous outfall, possessing a broad siliciclastic inner shelf, a thin transitional zone and a low gradient, extensive, dispersed stromatoporoid-coral bank tract grading seaward to coralline thickets.

FANNING RIVER AREA

This area incorporates the Fanning River Caves section (L791), Fanning River type section (L788) and sections to the north (L789/790). Maximum thickness of the Fanning River Group is attained in the vicinity of L791, and throughout this area the lower part of the group is diverse with a complex facies architecture. The interpreted facies mosaic (Fig. 7) forms the basis of a reconstructed palaeogeography presented in Fig. 8.

NON-MARINE ASSOCIATION

Non-marine units were mapped to the immediate north of the base of section L791. They outcrop poorly in restricted to a few shallow gullies, and consist of sandstones interbedded with red-brown shales. A better representation of non-marine strata occurs in section L789, where interbedded red shales and coarse clastics are prominently exposed within deep erosional gullies. The units are dominated by coarse arkose and are demonstrably discontinuous at both sites, suggesting restriction to topographic lows on the palaeosurface. It is succeeded by fossiliferous sandstone facies, highlighting the continuance of local siliciclastic input during the early deposition of marine units.

INNER SHELF ASSOCIATION

Topographic relief at the base of the Fanning River Group in the immediate Fanning River area (L788) was demonstrated by Wyatt (1973) and Wyatt and Jell (1980) and is confirmed in this work. It is shown to have a bearing on inshore facies architecture, particularly for the sequences displayed by the type section. The scale of relief in this area is illustrated in Fig. 7.

Lowermost abraded bioclast, siliciclastic facies is replaced by fossiliferous siltstone facies which lenses out to the immediate south, suggesting deposition in a relative topographic "low" of the palaeosurface. Such facies represent a silty embayment adjacent to granitic headlands. Increased numbers of branching coral assemblages suggest a wide seafloor tract, just inshore of the

biostromes where coralline forms flourished in a silty environment. Minor biostromes in these units shows patch reefoid development in a truly fringing setting.

To the north, fossiliferous sandstone facies is locally succeeded by impure limestone facies units, but units of both types are discontinuous. This suggests a palaeogeography in which some creek or river outfall was present near L789/790. Large volumes of coarse siliciclastics did not extend to L788 where finer grained sediments dominated the lower "pre-biostromal" depositional phase. There is, however a strong, fine siliciclastic signature to these lower units. Siliciclastic dominance at L791 is also suggestive of terrigenous outfall.

PROXIMAL SHELF ASSOCIATION

Lower parts of the sequence in the Fanning River area (L788) suggest that biostromal development took place very close to shore. To the immediate south of the type section biostromal units occur only a few metres above the unconformity, and show characteristically coarse siliciclastic-rich matrices. Within the type section, the lowermost biostromal units have silty matrices and developed adjacent to the embayment described above. All these lower units are locally discontinuous and probably never formed extensive banks. Higher in the sequence units become less terrigenous in content and more laterally extensive. Biostromal units are relatively thin and were, therefore, short-lived, having been terminated by emplacement of storm debris units or siliciclastic depositional pulses. Relationships between facies elements of the biostromal association in this area are complex (Fig. 9). Micritic stromatoporoid floatstone is interbedded with rubbly floatstone, rudstone and *Amphipora*-coral packstone. All units are laterally discontinuous. They represent the development of extensive stromatoporoid-brachiopod biostromes which were commonly reworked by storm events. Storm energy was sufficient to fragment most skeletal material *in situ*, or nearly so. The preponderance of these units attests to the frequency of storm reworkings in an otherwise quiet carbonate shelf setting. Such events probably restricted the development of a major bioherm in this area.

A 19m fining upwards sequence of rudstone passing to coverstone-wackestone within Fanning River Caves (L803, Fig. 10) is indicative of the thicknesses of biostromal "packages" in the Fanning River Caves area and attests to the high-energy reworking of biostromal units.

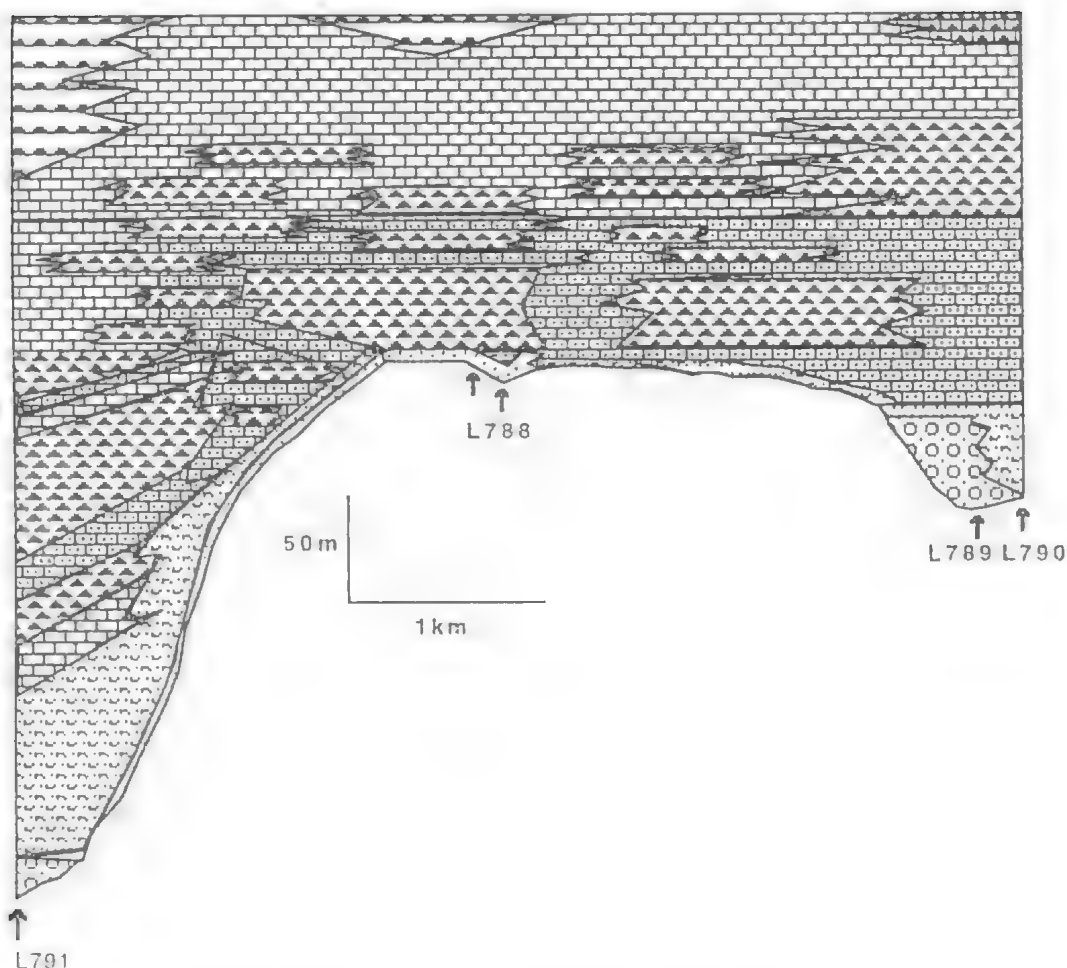


FIG. 7. Interpreted facies mosaic for the Fanning River area. Key as per Fig. 2.

Endophyllum siltstone facies within the uppermost interval of the sequence at Fanning River (L788) and Fanning River Caves (L791) represents the initiation of regression transitional to deposition of the Cultivation Gully Formation. This facies was deposited on the proximal shelf showing increasing siliciclastic input, with the development of isolated patch bioherms of corals and, rarely, stromatoporoids.

DISTAL SHELF ASSOCIATION

Coralline packstone associations are a testament to the maximum transgressive phase in this part of the subprovince. They are laterally extensive across the area and show the presence of

variable coralline thickets on the distal shelf. The development of distal shelf associations was punctuated by perturbations of relative sea-level which resulted in some biostromal formation as interbeds.

SUMMARY

The Fanning River Group in the Fanning River area is distinct from that displayed in the remainder of the subprovince, showing a general, quiet water biostromal accumulation, punctuated by siliciclastic pulses and storm reworking as rubble deposits. Variable thickness of the group in this area reflects differential subsidence consistent with the development of half grabens as sug-

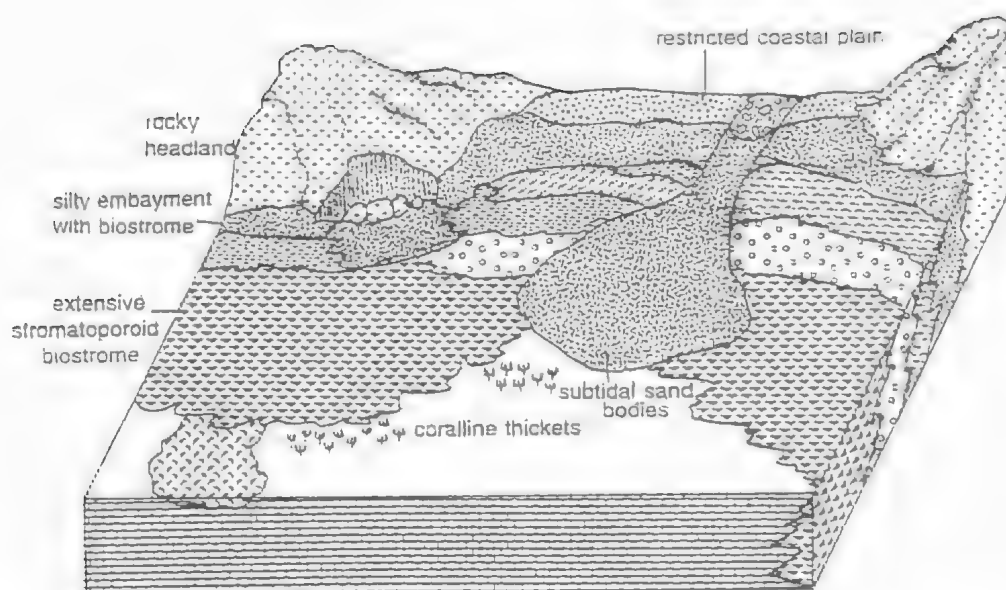


FIG. 8. Reconstructed palaeogeographic and depositional setting for Fanning River area. Key as for Fig. 2.

gested by previous authors (Wyatt & Jell, 1980; Lang et al., 1990). Distal facies are well developed and probably represent the maximum flooding of the subprovince, but there is no biostratigraphic confirmation of this suggestion. These facies are replaced by shallower water units showing an increasing siliciclastic influence during regression culminating in deposition of the Cultivation Gully Formation.

HORSESHOE BEND-GOLDEN VALLEY

INNER SHELF ASSOCIATION

Non-marine facies are well developed in and north of Golden Valley (L800), but are not present at or north-east of Horseshoe Bend. Fossiliferous sandstone facies is thickly and extensively developed within the Golden Valley area, and to the northeast of Horseshoe Bend. At Horseshoe Bend, siliciclastics are restricted to the lowermost few metres of sequence. At L786 this interval consists of granitoid conglomerate and at L787, coral-rich fossiliferous sandstone/conglomerate is present. These occurrences suggest a lowland infill of siliciclastic nonmarine strata in the Golden Valley area. To the west, at Horseshoe Bend, siliciclastic input was not high and was restricted to initial the depositional phase.

PROXIMAL SHELF ASSOCIATION

Poor outcrop within the Golden Valley area has restricted detailed analysis. Here inner shelf impure packstone is overlain by thin biostromal units. These indicate a rapid transition from coarse siliciclastic dominance to a modest in-shore mixed facies assemblage followed by a thin interval of biostromal development. Proximal facies developed at Horseshoe Bend are unlike that at Fanning River. They are dominated, particularly in upper units, by impure coral packstone and dispersed stromatoporoid packstone with rare coverstone. Increased siliciclastic input, associated with impure packstone terminated the minor phase of coverstone development.

DISTAL SHELF ASSOCIATION

Tabulate coralline packstone is relatively thin and is succeeded by a great thickness of micritic limestone. This is thought to represent a higher shelf gradient in the Golden Valley area and the representation of a somewhat deeper water environment in comparison with other parts of the basin.

SUMMARY

The Fanning River Group in the Golden Valley area is atypical. The lower siliciclastic facies are unusually thick, proximal shelf facies are poorly developed and distal shelf facies dominates the

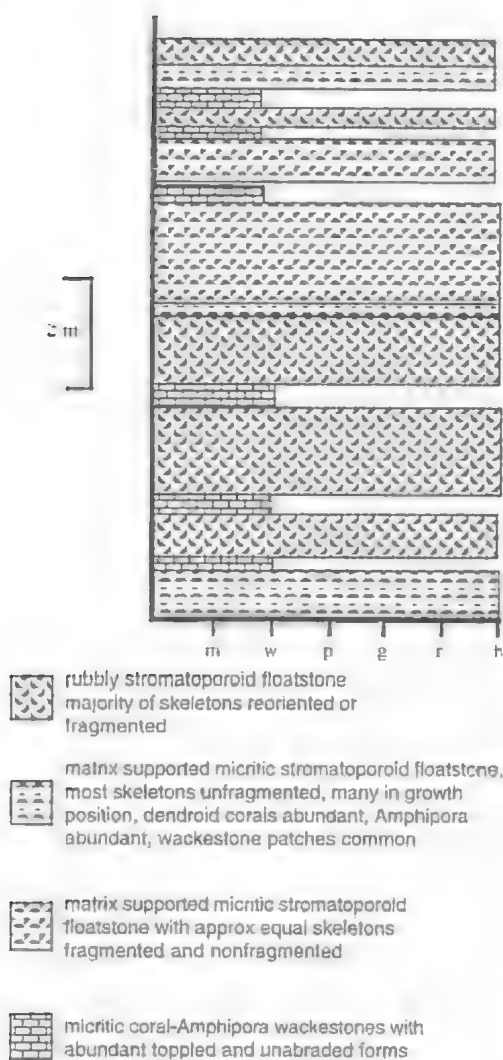


FIG. 9. Log of part of biostromal association relationships for part of section at L778.

upper part of the succession. This pattern suggests that active siliciclastic sedimentation dominated the inner shelf, restricting the development of inner shelf carbonate facies, and that proximal shelf facies deposition was rapidly replaced by a "deeper water" limestone accumulation during transgression.

The Horseshoe Bend sequence shows facies characters typical of both the Fanning River and Fletcherview areas. Basal siliciclastics are subordinate. Biostromal units are poorly developed and are succeeded by a siliciclastic pulse of sedimen-

tation. Carbonate deposition was dominantly in the form of proximal shelf pavements of dispersed stromatoporoids or offshore coralline thickets of packstone facies. There were no true reefal buildups.

KIRKLAND DOWNS

The sequence here rests upon metamorphic basement. Where measured it shows a moderate thickness of nonmarine siliciclastics, thin horizons of inner shelf siliciclastics and a moderately thick biostromal development, succeeded by thin, poorly exposed coralline packstone of distal shelf facies association. Siliciclastic units were localised, reflecting basement topography. The biostromal units developed within this area are atypical of the remainder of the the basin and the biostromal units contain an abundant, diverse colonial rugose coral fauna (Zhen, 1991). In addition, the sequence here is somewhat dolomitised making stromatoporoid identification difficult. The deposition of carbonate units within this area took place at the basin margin in an embayed setting. Conodont assemblages (Talant & Mawson, 1994) suggest restricted, or silled, basinal conditions for the Kirkland Downs area.

PAYNES LAGOON (BOUNDARY CREEK)

The Fanning River Group is restricted to a few metres of coral-quartz-metamorphic cobble conglomerate which overlies an undulating nonconformity surface atop metamorphics. Along strike to the west, impure tabulate coral packstone is present. There appears to be no *in situ* stromatoporoid-coral biostromal development, but, by inference, must have occurred nearby to source these rubble deposits. Furthermore localised tabulate coral thickets, formed in nearshore, quiet water embayments. At the western perimeter of outcrop, near Boundary Creek, the Fanning River Group is represented by a shell bed up to 5m thick in which large *in situ* *Modiomorpha mitchellae* Cook (1993a) form extremely localised bivalve clumps (*sensu* Kidwell, et al., 1986). The facies expressed in the Boundary Creek area probably represent high-stand basin margin deposits.

HERVEYS RANGE

Thin sequences of the Fanning River Group unconformably overlie the Argentine Metamorphics in a series of fault blocks stretching NW

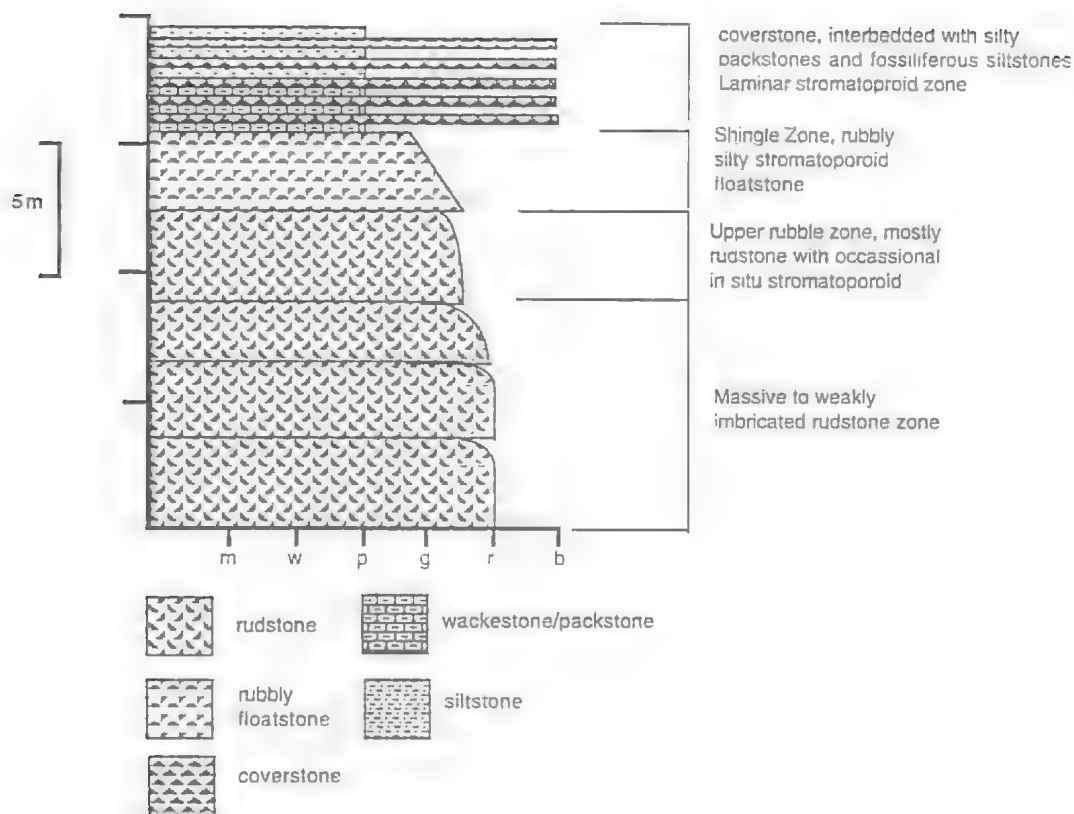


FIG. 10. Log of fining upwards succession exposed within Maternity Cave, JCUL803.

from near Keelbottom Creek (Dotswood 1:100 000 sheet, DU 305 398) to near Fortesque Creek at (Rollingstone 1:100 000 sheet, DU 449 351). Thin basal metamorphic conglomerates of the abraded bioclast, coarse clastic facies are overlain by thin fossiliferous siltstone and biostromal limestone. Other workers (Wyatt, 1973; Zhen, 1991) have provided some detail on these outcrops, highlighting the paucity of biostromal units and the abundance of silty sediments and basal coarse siliciclastics.

CALCIUM-REIDS GAP

A contact metamorphosed sequence of the Fanning River Group crops out in the Reids Gap-Calcium area and was recently quarried by North Australian Cement Limited. Within this area some sequence 350m of coarse marine siliciclastics, probably belonging to the fossiliferous sandstone facies, dominates a somewhat thinner

sequence of fossiliferous siltstone, biostromal limestone, and coralline packstone (Lang et al., 1990). Wyatt et al. (1970) noted abundant *Stringocephalus* biostromes in the area.

MINGELA BLUFF

Non-marine Collopy Formation located east of Mingela (Fig. 1) have been variably interpreted as Mesozoic (Wyatt et al., 1970) or Palaeozoic. It occupies the same stratigraphic position as the Fanning River Group, nonconformable upon Ravenswood Granodiorite. Lycopod and megaspore fossils indicate a Devonian age, no older than Middle Devonian. These units may be terrestrial equivalents of the Big Bend Arkose or may equate to a younger stratigraphic interval Burdekin Subprovince assemblage such as that represented by the Picadilly Formation (as suggested by Draper & Lang, 1994).

MOUNT PODGE

Strata within the Mount Podge area are herein regarded as part of an older depositional phase of the Burdekin subprovince (cf. Talent & Mawson, 1994) and are included only for regional completeness. Basal units in the Mount Podge area are divided into the Laroona Formation and Mount Podge Limestone (Zhen, 1991). Studies of these units by Pacholke (1992) and Zhen (1991) have revealed a thin, highly variable sequence which shows broad sedimentological analogies with the Fanning River Group. Basal clastics overlying Precambrian metamorphics are relatively thick. They consist of metamorphic clast conglomerates succeeded by sparsely fossiliferous pebbly sandstones in turn overlain by sparsely fossiliferous micaceous sandstone. These strata are interpreted as fluvial to shoreface deposits (nonmarine association, abraded bioclast coarse siliciclastic and fossiliferous sandstone facies respectively).

Inner shelf facies in the Mount Podge area are pebbly conglomerate, micaceous sandstone, *Xystriphyllum* floatstone, muddy coral-brachiopod wackestone/ packstone and intraclastic rudstone. Proximal shelf equivalents are represented by stromatoporoid coverstone, rudstone and floatstone. Distal shelf equivalents are crinoidal grainstone and uppermost coralline packstone.

Carbonate facies not represented in the lower Fanning River Group are intraclastic rudstone and quartz granule-coral floatstone. Lowermost carbonate units are highly impure, quartz granule-coral floatstone, representing nearshore *Xystriphyllum* biostromes and muddy impure coral-brachiopod packstone, representing quiet, inner shelf sedimentation. Intraclastic rudstones are developed near the base of the carbonate sequence and indicate early sea-floor lithification of muddy carbonate horizons and/or emergent shoaling in a nearshore environment. Bioherms are not developed in this area, but extensive biostromes of corals and laminar stromatoporoids and rudstones and floatstones attest to significant, high energy reworking of such units. Coral packstone and crinoidal grainstone developed seaward of the biostromes.

CARBONATE PRODUCTION

Primary carbonate sources during accumulation of the Burdekin Formation and Big Bend Arkose were coralline and shelly skeletal debris and the disintegration of codiacean (*Penicillus*-

like) algae to form lime mud. Major carbonate producers and sources for each facies association are tabulated (Table 8) and divided into allochthonous and autochthonous categories.

The primary source for carbonate in the inner shelf were the disintegration of codiacean algae to produce carbonate mud. According to Enos (1983) and James (1984), disintegration of codiacean algae is a primary source of lime mud within the "subtidal carbonate factory" of the modern shelf and was also a major source in the Devonian. Other sources of the inner shelf are molluscs, and dendroid corals.

The proximal shelf was dominated by robust skeletal carbonate production, mainly stromatoporoids, with a significant micrite contribution by algal disintegration.

Distal shelf facies carbonate was provided primarily by coralline and shelly faunas with micritic contribution from algae. Deeper water facies must have gained significant volumes of algally derived-muddy carbonate by transport from adjacent shallower, high-photoc zones of the shelf. However, in other facies the carbonate sources were mostly *in situ*, with only transport of carbonate to adjacent facies associations. Quiet water conditions and a biostromal complex in the proximal shelf would have provided some barrier to large-volume transport of carbonate across the shelf.

Bioeroders were present within the Burdekin depositional system and included algae, and probably fungi, as evidenced from widespread micrite rims on skeletal grains. Larger, cylindrical, "trypanitid" type borers, expressed by larger holes in some skeletons are also represented. Endolithic bioerosion has been qualitatively assessed for each facies based on the presence of micrite envelopes and presence of larger borings and micrite films between growth phases in skeletons of larger faunal elements. These are summarised in Table 9. Although some levels of bioerosion are present in all facies, it is clear that endolithic processes were not a dominant source of carbonate within this carbonate system, in comparison to modern reefal settings (Fagerstrom, 1987).

Bioerosion by the micritisation of skeletal grains within coralline packstone facies would have contributed moderate volumes of lime mud to other distal shelf facies. Bored skeletal grains are mechanically weakened (Bathurst, 1975), and more liable to disintegration. However the micrite thus derived cannot account for the volumes present in coralline packstone or micritic carbon-

TABLE 8. Carbonate sources and bioerosion within constituent facies of the Big Bend Arkose and Burdekin Formation.

| Facies | Autochthonous producers | Allochthonous components | Allochthonous sources | Rank importance of bioerosion |
|--|---|---|--|-------------------------------|
| Abraded Fossiliferous coarse siliciclastic | | molluscs, corals | subtidal sand bars, innershelf lagoon | Low |
| Fossiliferous sandstone | gastropods, bivalves, minor algae. Minor stromatoporoids and corals | corals, stromatoporoids | subtidal carbonate lagoon, proximal biostromes | Low |
| Fossiliferous siltstone | corals, algae, molluscs, brachiopods, stromatoporoids | minor stromatoporoids, corals | adjacent biostromes | Low-moderate |
| Nodular limestone | algae, corals, stromatoporoids, chaetetids | minor stromatoporoids, corals | adjacent biostromes | Low |
| Impure sandstone-limestone | algae, molluscs, corals, dendroid stroms | corals, stromatoporoids | adjacent lagoon and biostrome, some may be reworked from fossiliferous sand bodies | Low-moderate |
| Biostromal | Stromatoporoids, corals, algae, brachiopods, molluscs | material reworked within biostromal complex | minor reworking from flanking thickets | Low-moderate |
| Dispersed stromatoporoid packstone | Corals, algae, stromatoporoids, brachiopods, molluscs | material reworked <i>in situ</i> | n.a. | Low |
| <i>Endophyllum</i> siltstone | Corals, ?algae, stromatoporoids, brachiopods | material reworked <i>in situ</i> | n.a. | Low |
| Crinoidal grainstone | corals, stromatoporoids, molluscs | coralline debris, crinoids, molluscan and brachiopod debris | coralline packstones, some debris from biostrome | Moderate-Pervasive |
| Coralline packstone | corals, algae stromatoporoids, brachiopods, molluscs, crinoids | as above derived within thicket complex | some derived from adjacent biostromal complex | Moderate |

ate facies. Thus, much of the micrite for these facies must have been derived from codiacean algae.

DEPOSITIONAL SUMMARY

Heterogeneity of depositional style, thicknesses and the absence of basin-wide units reflect significant basement topography at the time of transgression interpreted as reflecting half-grabens (Lang et al., 1990) which were actively forming during deposition. Initial transgression was upon a surface with at least 300m of local relief (Figs 6-8). Restricted coastal plains were developed in local depositional hollows.

The siliciclastic to carbonate transition was rapid, but incomplete, across the inner and proximal shelf resulting in the heterogeneous sedimentary assemblage. Coarse clastic deposition

was confined to immediate inshore areas (Figs 6; 8), proximal to stream outfall, but siliciclastic pulses spasmodically strayed onto the proximal shelf. Carbonate lagoons, less than 5m in depth, developed within the inner shelf, leeward of biohermal and biostromal buildups and contained scattered, small patch reefs or bommies. Two styles of large-scale, stromatoporoid-dominated, buildup formed in the proximal shelf: low bioherm (Fig. 6) and extensive biostrome (Fig. 8). Both formed under quiet water conditions punctuated by storm or other high energy events. Water depths were shallow, as little as 1-2m. Buildups occupied zones from innermost shelf adjacent to the shoreline, to a few kilometres offshore and were heavily influenced by siliciclastic sedimentation which commonly resulted in their termination. In places, stromatoporoid buildups and biostromes were

TABLE 9. Rank abundance of micritised grains within lithological samples within the Big Bend Arkose and Burdekin Formation: L = low, M = moderate, A = abundant, P = predominant.

| Facies | Samples | Micritised grain abundance |
|-------------------------------------|-----------|----------------------------|
| Coarse siliciclastic, marine facies | JCUR32164 | L |
| | JCUR34934 | L |
| | JCUR34935 | M |
| | JCUR34940 | L |
| | JCUR34992 | L |
| Fossiliferous siltstone facies | JCUR34938 | L |
| | JCUR34945 | L |
| | JCUR34949 | L |
| | JCUR34950 | L |
| Nodular limestone facies | JCUR32113 | M-A |
| | JCUR32113 | L-M |
| | JCUR32179 | M |
| | JCUR32180 | L |
| Impure limestone-sandstone | JCUR32135 | L |
| | JCUR34918 | L |
| | JCUR34921 | L-M |
| | JCUR34922 | M |
| | JCUR34923 | M |
| Biostromal facies | JCUR34951 | L-M |
| | JCUR34970 | L-M |
| | JCUR34967 | L-M |
| | JCUR34957 | L |
| | JCUF11407 | L |
| | JCUF11409 | L |
| Coralline packstone facies | JCUR32116 | M |
| | JCUR32117 | M |
| | JCUR32118 | A |
| | JCUR34895 | L-M |
| | JCUR34896 | M |
| | JCUR34898 | M |
| | JCUR34978 | M |
| Crinoidal grainstone | JCUR32126 | A-P |
| | JCUR32127 | A-P |
| | JCUR32128 | A |
| | JCUR32129 | A-P |

poorly represented. Instead scattered stromatoporoid pavements formed on the proximal shelf in quiet, shallow water, removed from turbulent disturbance. Seaward of major buildups and banks lay tracts of coralline and *Amphipora* thicket (Figs 6,8), and crinoidal sand bodies distributed across a siliciclastic-poor, shallow, shelf (Fig. 6). Coralline packstone facies represents the maximum transgressive phase for much of the subprovince and was deposited in variable depths, probably down to 25-30m.

Local carbonate mudstone represents deeper water, "basinal" facies with water depths possibly as much as 80m. Coral patch reefs grew in increasingly siliciclastic settings during initial regression to the overlying Cultivation Gully Formation.

Four characteristics of the Fanning River Group are striking: (1) the high siliciclastic component of the "reefal" system. (2) the quiet water style of deposition, punctuated by high energy

events. (3) the near absence of emergent carbonate facies. (4) large thickness variation of the group.

Highly siliciclastic biohermal and biostromal facies can be attributed to proximity to the shoreline and terrigenous sediment source. Thus reefal tracts truly represent fringing reefs. Such reefs are well known from the fossil record (e.g. Playford, 1980; Santisteban & Taberner, 1988; Braga Martin & Alcalá, 1990) and are well documented in modern environments (e.g. Johnson & Carter, 1987; Johnson & Risk, 1987). Fringing reefs form in a range of different settings: attached to islands or the mainland coast (Johnson & Carter, 1987), adjacent to headlands upon terrigenous sandy and muddy substrates (Johnson & Risk, 1987; Johnson & Carter, 1987), or upon coarse delta lobes (Hayward, 1982; Braga, Martin & Alcalá, 1990). For the Burdekin Formation, biostromes developed within quiet clastic bays adjacent to headlands upon muddy substrates, in shallow mixed-carbonate lagoons proximal to coarse siliciclastic shorelines, and in biohermal and biostromal settings, in nearshore mixed carbonate-siliciclastic muddy lagoons.

The abundance of quiet water deposits, punctuated by units representing high energy reworking within the biostromal complex suggests that quiet conditions were the norm with storm conditions sufficiently frequent as to allow thick accumulations of stromatoporoid and coralline biostrome. This highlights the importance of storm or high energy events on the shelf (Kreisa, 1981) particularly on inner and proximal shelf processes (Gagan, Chivas & Henczeg, 1990; Racki, 1993). Storm reworking provided a significant proportion of biostromal units within the Fanning River Group.

The juxtaposition of quiet and high energy deposits interpreted as having been deposited in very shallow water implies that fair weather wave base was very shallow or that most of the inner and proximal shelf was protected. Since no high relief barrier appears to have existed, fairweather wave energy must have been constrained, suggesting a limited fetch for wind generated waves. The Burdekin Basin appears to have been largely isolated from the Palaeo-Pacific ocean to the east, and internally, the Dotswood High (Wyatt & Jell, 1980) would have further constrained wind generation of waves within the basin. Talent & Mawson (1994) have suggested elements of the basin were silled, based on conodont analyses.

The absence of emergent shoaling facies within the carbonate sequence is anomalous in compar-

ison with other shallow water carbonate systems (Read, 1973; Laporte, 1967). Accumulation must have matched the subsidence rate following the initial rapid transgression. Detailed analysis of cyclicity within the sequence would provide a much more detailed depositional history, but has not been attempted here. There were however depositional pulses at the scale of tens of metres, particularly in the Fanning River area, where biostromal units are interstratified with mixed carbonate-clastic facies, or poorly exposed units with elevated siliciclastic impurities. These may reflect minor tectonic movements along basement faults providing clastic pulses into the depositional system during the gentle rifting of the subprovince (Draper & Lang 1994).

The large differences in thickness across the sub province attest not only to relief of the transgressed palaeosurface, but also differential subsidence within the half-graben systems (Lang et al., 1990).

The conodont data of Talent & Mawson (1994) place timing of maximum transgression is as well within the Givetian *varcus* zone for the eastern basin. This is based on presence of late *varcus* zone conodonts from the upper part of the type section. Timing of the initial transgression is problematic. *Stringocephalus* has been recovered in abundance from the basal Burdekin Formation adjacent to the type section (31 m above base), but there are no diagnostic conodonts below 119 m for the type section. These lowermost index conodonts indicate a middle *varcus* age, but are quickly replaced by late *varcus* age taxa some 5 m above. The *varcus* zone may extend well below the 119 m level (Talent & Mawson, 1994). Using these data and the presence of *Stringocephalus* sp., the bulk of the Fanning River Group type section must be Givetian, and the 31-119 m interval must be within the *hemiansatus* to Early-middle *varcus* zone. Data on the Burdekin Downs section indicate a pre-late *varcus* deposition for the lower half of that sequence. It therefore appears that transgression may have begun in the ?latest Eifelian to earliest Givetian, but the majority of carbonate deposition took place within Givetian, prior to the *hermanni-cristatus* zone. Maximum transgression occurred within the late *varcus* zone.

Timing of deposition at basin margins is controlled by presence of *varcus* zone conodonts from Turtle Creek on the Herveys Range (Zhen, 1991) and the presence of ?late *ensensis* to early *varcus* forms within the Kirkland Downs area.

Deposition in the Mount Podge area mostly predates the Burdekin sequence proper. Greater biostratigraphic control for this sequence indicates *serotinus* zone to *costatus* zone ages for most of it, but there is a single occurrence of an at least early *varcus* zone conodont in the upper parts of one Mount Podge section (Talent & Mawson, 1994) indicating a possible Givetian depositional phase. There may be two depositional packages in the Mount Podge sequence with the younger package, probably corresponding to the Fanning River Group further south, mostly removed by erosion prior to deposition of the Myrtlevale Formation, although there is only questionable stratigraphic evidence for this at Mt Podge.

Unfortunately the absence of high resolution biostratigraphic control on deposition prohibits estimates of the rate of transgression, subsidence, contemporaneous fault movements, individual buildup events, or subsequent regression. Eastern Australian transgressive cycles during the Devonian have been discussed by Talent & Yolkin (1987) and Talent (1989) who commented that the *varcus* zone transgression had not been recognised in Australia. Regression in the middle to upper *varcus* zone within the Mytton Formation, Broken River Province (Talent & Yolkin, 1987; Talent, 1989) appears to predate regression to the Cultivation Gully Formation in the Burdekin Subprovince.

ACKNOWLEDGEMENTS

Bob Henderson of the Geology Department of James Cook University is thanked for assistance and provision of grants during 1989-1994. Peter Jell, John Jell, Mary Wade and Trevor Clifford are thanked. Natalie Camilleri & Donna Case are thanked for their assistance with diagrams. I am grateful to the Queensland Museum for support.

LITERATURE CITED

- ALLEN, J. R. L. 1974. Studies in fluvial sedimentation: Implications of pedogenic carbonate units in the Lower Old Red Sandstone Anglo-Welsh outcrop. *Geological Journal* 9: 181-208.
- BALL, M. M. 1967. Carbonate sand bodies of Florida and the Bahamas. *Journal of Sedimentary Petrology* 37(2): 556-591.
- BATHURST, R. G. C. 1971. Carbonate sediments and their diagenesis. (Elsevier: Amsterdam). 658p.
- BELPERIO, A. P. & SEARLE, D. E. 1988. Terrigenous and carbonate sedimentation in the Great Barrier Reef Province. Pp. 143-174 in Doyle, L. J. & Roberts, H. H. (eds.) *Carbonate-Clastic Transi-*

- tions. *Developments in Sedimentology* 42 (Elsevier: Amsterdam).
- BJERSTEDT, T. W. FELDMANN, R. M. 1985. Stromatoporoid paleosynecology in the Lucas dolomite (Middle Devonian) on Kelleys Island, Ohio. *Journal of Paleontology* 59(5): 1033-1061.
- BRAGA, J. C. MARTIN, J. M. & ALCACA, B. 1990. Coral Reefs in coarse-terrigenous sedimentary environments (Upper Tortonian, Granada Basin, southern Spain). *Sedimentary Geology* 66:135-150.
- BURCHETTE, T. P. 1981. European Devonian reefs: A review of current concepts and models. Pp. 85-142 In Toomey, D. F. (ed.) *European Fossil Reef Models. Society of Economic Paleontologists and Mineralogists Special Publication* 50.
- COOK, A. G. 1993a. Two bivalves from the Middle Devonian Burdekin Formation. *Memoirs of the Queensland Museum* 33(1): 49-53.
- 1993b. *Fletcheriella septata*: A new high-spined septate gastropod from the Devonian of North Queensland. *Journal of Paleontology* 67(5): 816-821.
- DRAPER, J. J. & LANG, S. C. 1994. Geology of the Devonian to Carboniferous Burdekin Basin. *Queensland Geological Record* 1994/9.
- DUNHAM, R. J. 1962. Classification of carbonate rocks according to depositional texture. *American Association Petroleum Geologists Memoir* 1: 108-121.
- EMBRY, A. F. & KLOVAN, J. E. 1971. A Late Devonian Reef Tract on Northeastern Banks Island, N.W.T. *Bulletin of Canadian Petroleum Geology* 19(4): 730-781.
- ENOS, P. 1983. Shelf. Pp. 267-296. In Walker, R. G. (ed.) *Facies Models. Geoscience Canada Reprint Series* 1.
- FAGERSTROM, J. A. 1987. The evolution of reef communities. (Wiley & Sons: New York).
- FLOOD, P. G. & ORME, G. R. 1988. Mixed siliciclastic/carbonate sediments of the Northern Great Barrier Reef Province, Australia. Pp.175-206 In Doyle, L. J. & Roberts, H. H. (eds.) *Carbonate-Clastic Transitions. Developments in Sedimentology* 42. (Elsevier: Amsterdam).
- FOLK, R. L. 1974. *Petrology of sedimentary rocks.* (Austin: Hemphills).
- FRIEDMANN, G. H. 1988. Histories of coexisting reefs and terrigenous sediments: The Gulf of Elat (Red Sea), Java Sea, and Neogene Basin of the Negev, Israel. Pp. 77-97. In Doyle, L. J. & Roberts, H. H. (eds.) *Carbonate-Clastic Transitions. Developments in Sedimentology* 42. (Elsevier: Amsterdam).
- GAGAN, M. K., CHIVAS, A. R. & HERCZEG, A. L. 1990. Shelf-wide erosion, deposition and suspended sediment transport during cyclone Winifred, Central Great Barrier Reef, Australia. *Journal of Sedimentary Petrology* 60(3): 456-470.
- HARDIE, L. A. & GINSBURG, R. N. 1977. Layering Pp. 50-122 In Hardie, L. A. (ed.) *Sedimentation on the Modern Carbonate Tidal Flats of Northwest Andros Island, Bahamas.* Johns Hopkins University Studies in Geology, No. 22. (Johns Hopkins University Press: Baltimore).
- HARRINGTON, R. J. 1987. Lithofacies and biofacies of the Middle and Upper Devonian Sultan Formation at Mountain Springs, Clark County, Nevada: Implications for stromatoporoid paleoecology. *Journal of Paleontology* 61(4): 649-662.
- HAYWARD, A. B. 1982. Coral reefs in a clastic sedimentary environment: Fossil (Miocene, S. W. Turkey) and modern (Recent, Red Sea) analogues. *Coral Reefs* 1:109-114.
- HEIDECKER, E. 1959. Middle Devonian molluscs from the Burdekin Formation of North Queensland. Department of Geology, University of Queensland. *Papers* 5(2): 1-11.
1960. The Regional and Economic Geology of the Dalrymple District. Hons. Thesis. Univ. Qld. (Unpubl.)
- JACK, R. L. 1879a. Report on the geology and mineral resources of the District between Charters Towers Goldfield and the Coast. Geological Survey of Queensland Publication 1: 1-28.
- 1879b. Preliminary Report relating to geological features of part of the coast range between the Dalrymple and Charters Towers roads. Geological Survey of Queensland Publication 2: 1-3.
1886. Handbook of Queensland Geology. Geological Survey of Queensland Publication 31.
- JACK, R. L. & ETHERIDGE, R. 1892. Geology and Palaeontology of Queensland and New Guinea. Geological Survey of Queensland Publication 82.
- JAMES, N. P. 1983. Reefs. Pp. 345-462. In Scholle, P. A., Bebout, D. G. & Moore, C. H. (eds.) *Carbonate Depositional Environments. American Association of Petroleum Geologists Memoir* 33.
1984. Reefs. Pp. 229-244 In Walker, R. G. (ed.) *Facies Models. Geoscience Canada Reprint Series* 1.
- JOHNSON, D. P. & CARTER, R.M. 1987. Sedimentary Framework of Mainland Fringing Reef Development, Cape Tribulation Area. Great Barrier Reef Marine Park Authority. Technical Memorandum 14.
- JOHNSON, D. P. & RISK, M. J. 1987. Fringing Reef Growth on a Terrigenous mud foundation, Fantome Island, Central Great Barrier Reef, Australia. *Sedimentology* 34: 275-287.
- JOHNSON, M. E. 1988a. Hunting for ancient rocky shores. *Journal of Geological Education* 36: 147-154.
- 1988b. Why are ancient rocky shores so uncommon? *Journal of Geology* 96: 469-480.
- KANO, A. 1990. Species, morphologies and environmental relationships of the Ludlovian (Upper Silurian) stromatoporoids on Gotland, Sweden. *Stockholm Contributions in Geology* 42(2): 85-121.
- KERSHAW, S. & RIDING, R. 1978. Parameterisation of stromatoporoid shape. *Lethaia* 11: 233-242.

- KLOVAN, J. E. 1974. Development of western Canadian reefs and comparison with Holocene analogues. *American Association of Petroleum Geologists Bulletin* 58: 787-799.
- KREBS, W. 1974. Devonian carbonate complexes of Central Europe. Pp. 155-203 In Laporte, L. F. (ed.) *Reefs in Time and Space*. Society of Economic Paleontologists and Mineralogists Special Publication 18.
- KIDWELL, S. M., FURSICH, F. T. & AIGNER, T. 1986. Conceptual framework for the analysis and classification of fossil concentrations. *Palaios* 1: 228-238.
- KREISA, R. D. 1981. Storm-generated sedimentary structures in subtidal marine facies with examples from the middle and upper Ordovician of southwestern Virginia. *Journal of Sedimentary Petrology* 51(3):823-848.
- LANG, S. C., FLEMING, P. J. G., JELL, J. S., ZHEN, Y. Y., & COOK, A. 1990. The Devonian-Carboniferous intracratonic Burdekin Basin, north Queensland. 1. Carbonate Siliciclastic Facies of the Fanning River Group. *Proceedings Pacific Rim Congress 1990* 3: 621-643.
- LAPORTE, L. F. 1967. Carbonate deposition near mean sea level and resultant facies mosaic: Manlius Formation (Lower Devonian) of New York State. *American Association of Petroleum Geologists Bulletin* 51(1): 73-101.
- LEAVITT, E. M. 1968. Petrology, Palaeontology, Carson Creek North reefs complex, Alberta. *Bulletin of Canadian Petroleum Geology* 16(3): 298-413.
- LECOMPTE, M. 1970. Die Riffe im Devon der Ardennen und ihre Bildungsbedingungen: Marburg. *Geologica et Palaeontologica* 4: 25-71.
- LEICHHARDT, L. 1847. *Journal of an Overland Expedition in Australia from Moreton Bay to Port Essington during the Years 1844-5*. (Boone: London).
- LONGMAN, M. W. 1981. A process approach to recognizing facies of reef complexes. Pp. 9-40 In Toomey, D. F. (ed.) *European Fossil Reef Models*. Society of Economic Paleontologists and Mineralogists Special Publication 50.
- MIALL, A. D. 1984. Deltas. Pp. 105-117 in Walker, R. G. (ed.) *Facies Models*. Geoscience Canada Reprint Series 1.
- MOLLER, N. K. & KVINGAN, K. 1988. The genesis of nodular limestones in the Ordovician and Silurian of the Oslo Region (Norway). *Sedimentology* 35: 405-420.
- MOUNT, J. F. 1984. Mixing of siliciclastic and carbonate sediments in shallow shelf environments. *Geology* 12: 432-435.
- NOBLE, J. P. A. 1970. Biofacies analysis, Cairn Formation of Miette reef complex (Upper Devonian) Jasper National Park, Alberta. *Bulletin of Canadian Petroleum Geology* 18(4): 493-543.
- PACHOLKE, D. 1992. The Geology of the Mount Podge Area. B. Sc. (Hons) thesis, James Cook University of North Queensland, (Unpubl.).
- PLAYFORD, P. E. 1980. Devonian "Great Barrier Reef" of Canning Basin, Western Australia. *American Association of Petroleum Geologists Bulletin* 64(6): 814-840.
- RACKI, G. 1986. Brachiopod ecology of the Devonian carbonate complex and problem of brachiopod hyposalinity. Pp. 363-373 In Racheboeuf, P. R. & Emig, C. C. (eds.) *Les Brachiopodes fossiles et actuels*. *Biostratigraphie du Paléozoïque* 4.
1993. Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37 (2-4): 87-182.
- READ, J. F. 1973. Paleo-environments and Paleogeography. Pillara Formation (Devonian), Western Australia. *Bulletin of Canadian Petroleum Geology* 21(3): 344-394.
- REINECK, M. E. & SINGH, J. B. 1980. *Depositional Sedimentary Environments*. (Springer-Verlag: Berlin).
- REINSON, G. H. 1984. Barrier Island and associated Strand Plain Systems. Pp. 119-140 In Walker, R. G. (ed.) *Facies Models*. Geoscience Canada Reprint Series 1.
- RIDING, R. 1981. Composition, structure and environmental setting of Silurian bioherms and biostromes in northern Europe. Pp. 41-83 In Toomey, D. F. (ed.) *European Fossil Reef Models*. Society of Economic Paleontologists and Mineralogists Special Publication 50.
- ROBERTS, H. H. 1987. Modern carbonate-siliciclastic transitions: Humid and tropical examples. *Sedimentary Geology* 50: 25-65.
- ROBERTS, H. H. & MURRAY, S. P. 1988. Gulfs of Northern Red Sea; depositional settings of distinct siliciclastic-carbonate interfaces. Pp. 99-142 In Doyle, L. J. & Roberts, H. H. (eds.) *Carbonate-Clastic Transitions*. *Developments in Sedimentology* 42. (Elsevier: Amsterdam).
- SANTISTEBAN, C. & TABERNER, C. 1988. Sedimentary models of siliciclastic deposits and coral reef interrelation. Pp. 35-76 In Doyle, L. J. & Roberts, H. H. (eds.) *Carbonate-Clastic Transitions*. *Developments in Sedimentology* 42. (Elsevier: Amsterdam).
- TALENT, J. A. 1989. Transgression-Regression Pattern for the Silurian and Devonian of Australia Pp 209-219 in Le Maitre, R. W. (ed.) *Pathways in Geology: Essays in Honour of Edwin Sherbon Hills*.
- TALENT, J. T. & MAWSON, R. 1994. Conodonts in relation to age and environmental framework of the Burdekin Basin (Mid-Devonian), north-eastern Australia. *Courier Forschungsinstitut Senckenberg* 168: 61-81.
- TALENT, J. A. & YOLKIN, E. A. 1987. Transgression-Regression patterns for the Devonian of Australia and Southern West Siberia. *Courier Forschungsinstitut Senckenberg* 92: 235-249.
- TSIEN, H. H. 1981. Ancient reefs and reef carbonates. *Proceedings of the 4th International Coral Reef Symposium, Manila* 1: 601-609.

- WAHLSTROM, E. E. 1948. Pre-Fountain and recent weathering on Flagstaff Mountain near Boulder Colorado. *Geological Society of America Bulletin* 59: 1173-1190.
- WALKER, R. G. 1984. Shelf and Shallow Marine Sands. Pp. 141-170 in Walker, R. G. (ed.) *Facies Models*. Geoscience Canada Reprint Series 1.
- WENT, D. J. 1991. Basement weathering at the Lower Palaeozoic unconformity in the Channel Islands and northern Brittany. *Proceedings of the Ussher Society* 7: 396-401.
- WILLIAMS, G. E. 1968. Torridonian weathering and its bearing on Torridonian palaeoclimate and source. *Scottish Journal of Geology* 4: 164-184.
- WILSON, J. L. 1974. Characteristics of carbonate platform margins. *American Association of Petroleum Geologists. Bulletin* 58 (5): 81-824.
- WYATT, D. H. 1973. The Stratigraphy and Palaeogeography of the Fanning River-Burdekin Downs-Star Area. M.Sc. Thesis (Unpubl.) James Cook University.
- WYATT, D. H. & JELL, J.S. 1980. Devonian and Carboniferous Stratigraphy of the northern Tasman orogenic zone in the Townsville Hinterland, North Queensland. pp. 201-228. In Henderson, R. A. and Stephenson, P. J. (eds.) *The Geology and Geophysics of Northeastern Australia*. (Geological Society of Australia, Queensland Division: Brisbane).
- WYATT, D. H., PAINE, A. G. L., CLARKE, D. E. & HARDING, R. R. 1970. Geology of the Townsville 1:250,000 Sheet area, Queensland. Bureau of Mineral Resources Report No. 127.
- ZEIGLER, W. 1979. Historical subdivisions of the Devonian p. 23-47 in House, M. R., Scrutton, C. T. & Bassett, M. G.(eds.) *The Devonian System*. Special Papers in Palaeontology 23.
- ZEIGLER, W. & KLAPPER, G. 1985. Stages of the Devonian system. *Episodes* 8: 104-109.
- ZHEN, Y. Y. 1991. Devonian Rugose Coral Faunas and Biostratigraphy of the Fanning River Group, North Queensland. Univ. Qld. Ph.D Thesis (Unpubl.).

APPENDIX

LIST OF LOCALITIES.

Localities refer to register numbers for Department of Earth Sciences, James Cook University of North Queensland. Grid references are from the Dotswood 1:100 000 topographic sheet, unless stated.

L778 Fletcherview station, east side of Burdekin River, downstream from "Little Rocks". Section from base of Fanning River Group to approximately 45m up sequence. Dotswood 1:100 000 DU 155027 to DU 157029.

L779 Fletcherview Station, north bank of Burdekin River upstream from "Little Rocks". Section from DU 149025 to DU 144027.

L780 Fletcherview Station, west bank of Burdekin River, downstream from Little Rocks. Section from lower Burdekin Formation, upwards (NE) 40m. DU 153030 to DU 157031.

L781 Burdekin Downs Station, North Bank of Burdekin River downstream from confluence of Arthurs Creek. Section from lower Burdekin Formation at DU 171032 to top of prominent cliffs at DU 169035.

L782 Western equivalent of main framestone unit in L781 at DU 167036, downstream from confluence of Arthurs Creek, Burdekin River, Burdekin Downs Station.

L783 Small un-named tributary of Arthurs Creek, joining at western side of Arthurs Creek near confluence with Burdekin River at DU 165040. Burdekin Downs Station Creek bank section of Big Bend Arkose.

L784 North bank of Burdekin River, Burdekin Downs Station, approximately 2km upstream from homestead. A short section through the Big Bend Arkose-Burdekin Formation transition at DU 180024.

L786 Tributary of Fanning River at Horseshoe Bend west of Horseshoe Bend Mill, Fanning River Station. Short section from unconformity to lower Burdekin Formation at DU 428105.

L787 North Bank of Fanning River at Horseshoe Bend, section along River running east to west from DU 425105 to 418103 along river flat.

L788 Fanning River Type Section, Fanning River, Upstream from Fanning River Station from DU 422204 to DU 417202.

L789 Fanning River North Section, approximately 3km N of Fanning River type section, in gullies from DU 419232 through forest clearing at DU 413230 to DU 410230. Big Bend Arkose to uppermost Burdekin Formation.

L790 Section in gully approximately 3km N of Fanning River Type section, through Big Bend Arkose and lowermost Burdekin Fmn. From DU 417228 to DU 414229.

L791 Section across main limestone hills SE of Fanning River type section, comprising all of the Burdekin Formation at its thickest representation. DU 448194 to DU 433178.

L792 Big Bend, Burdekin River, Burdekin Formation only from DU 093055 to DU 091052.

L793 Outcrop in un-named Creek from base of Fanning River Group at DU 185 026 upstream for approx 100 metres. Burdekin Downs Station.

L794 Isolated rubblecrop containing abundant well preserved stromatoporoids, N of L781 at DU 176037 Burdekin Downs Station.

L796 Kirkland Downs, immediately S of road into property at Hillgrove 1:100 000 sheet 993604.

L798 Paynes Lagoon Station, 200m south of Boundary Creek, approximately 800m to the west of cattle yards at 045 467 Rollingstone sheet.

L800 In Hills 1km NNW of Golden Valley. Section through Big Bend arkose from DU 451115 to 448113. L801 Mount Podge, Laroona Station. Section from northern edge of rhyolite intrusion to top of Mount Podge Limestone along Running Creek. Laroona Formation and Mount Podge Limestone.

L802 Mount Podge Eastern section. Approximately 600m E of Running Creek Section from basal sandstones East of un-named gully N to same Gully, offset 200m E in gully and thence N to base of Keelbottom Group at foot of hill.

L803 Fanning River Caves, Rope Ladder Cave, 18m section of Burdekin Formation, through three main chambers. 3km SE of Fanning River Station; part of L791 section.

L805 Arthurs Creek, small section through basal units at Dotswood DU169048.

L806 Fletcherview, immediately N of section L778, small section in cliffs across river from L781/2.

FOSSIL RECORD OF A VARANID FROM THE DARLING DOWNS, SOUTHEASTERN QUEENSLAND. *Memoirs of the Queensland Museum* 38(1):92. 1995:- Knowledge of the fossil lacertilians of Queensland is scant. (Molnar, 1991). In Queensland, fossil varanids are known from the Darling Downs, Riversleigh, Dry River, Tea Tree Cave, "Glen Garland" swamp deposits, and unnamed beds at Floraville, Cape River and Springsure. (Molnar, 1991: 669-671). Material is registered at the Queensland Museum.

Two vertebrae in the fossil varanid collection were found to be unlike those of *Megalania* but similar to caudal vertebrae of water monitors. These fossils lack precise collection data but have characteristic preservation typical of material from Plio-Pleistocene sites of the Chinchilla Rifle Range and numerous sites from King Creek. Furthermore, they were boxed with *Megalania* vertebrae labelled 'C20', indicating a Chinchilla Rifle Range locality. Thus the fossils are most probably from either the eastern or western Darling Downs. This material further documents the existence of varanids other than *Megalania* on the Darling Downs.

These vertebrae are easily referred to *Varanus* due to their general form; differing in size from, and lacking the robust

base of the neural spine evident in *Megalania* vertebrae. They were compared with those from several extant *Varanus* species (Table 1).

Similarities with *V. mertensi* are obvious (Table 1) but strong similarities also exist with *V. panoptes*. Given limited comparative material; and the similarity of caudals of the two groups, I am restricted to the conclusion that the fossils belong to a species related to *V. mertensi* or *V. panoptes*. Both of these species live in well-watered conditions unlike those existing today on the Darling Downs.

Acknowledgement

I thank Ralph Molnar and Jeanette Covacevich for their advice.

Literature Cited

MOLNAR, R. E. 1991. Fossil reptiles in Australia. Pp. 605-702 In Vickers-Rich, P., Monaghan, J. M., Baird, R. F. & Rich, T. H. (eds.), *Vertebrate Palaeontology of Australasia*. (Pioneer Design Studio: Lilydale).

Joanne Wilkinson, Queensland Museum, PO Box 3300, Brisbane, Queensland 4101, Australia; 23 February 1995.

TABLE 1. Comparison of key characters with selected modern *Varanus* spp. O= present, X= absent, *= not available

| Characters | Varanus spp. | | | | | | |
|---|---------------------------------|--------------------------------|--------------------------------|--------------------------------|------------------------------|----------|------------|
| | Modern | | | | | Fossil | |
| | <i>V. giganteus</i> QMJ17565 | <i>V. mertensi</i> QMJ46280 | <i>V. panoptes</i> QMJ48291 | <i>V. salvator</i> QMJ14498 | <i>V. varius</i> QMJ15361 | QMF31815 | QMF31816 |
| neural spine vertical | * | o | o | x | x | o | o |
| ratio of neural spine height to central length 0.5-0.8 | x | o | o | x | x | o | o |
| anterior tip of neural spine wedge shaped and laterally crenulated | x | o | x | x | x | o | tip eroded |
| neural spine slightly constricted basally | o | o | o | o | o | o | o |
| anterior margin of neural spine near midline of centrum | x | o | o | o | o | x | o |
| ridge from neural spine to prezygapophisal processes forms a triangular basin | * | o | o | o | o | o | o |
| two sharp ridges enclosing central groove on ventral surface of centrum | * | o | x | x | o | o | x |
| zygapophisal facets oriented between 35-45° | * | o | o | o | x | o | o |
| transverse process on central caudal declined | * | o | x | x | o | o | o |

A TINY CRIBELLATE SPIDER, *JAMARA* GEN. NOV. (ARANEAE:
AMAUROBIOIDEA: MIDGEEINAE) FROM NORTHERN QUEENSLAND.

VALERIE TODD DAVIES

Davies, V. Todd, 1995 06 01: A tiny cribellate spider, *Jamara* gen. nov. (Araneae: Amaurobioidea: Midgeeinae) from northern Queensland. *Memoirs of the Queensland Museum* 38(1): 93-96. Brisbane, ISSN 0079-8835.

Tiny cribellate *Jamara* gen. nov. is related to ecribellate *Midgee*, Davies, 1995. It adds another taxon to the complex assemblage of Australian amaurobioids. □ *New genus, new species, Jamara pisinna* sp. nov., north Queensland, amaurobioids.

Valerie Todd Davies, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 22 Aug 1994.

In a recent paper (Davies, 1995) described nine species of a tiny ecribellate litter spider, *Midgee*. The cribellate described here is similar in size and appearance and is classified as a 'midgeeine'.

Spiders were all collected from moss on tree trunks or rocks at altitudes between 1500-1560m on Mts Bellenden Ker and Bartle Frere, north Queensland. Notation of spines follows Platnick and Shadab (1975). All material is lodged in the Queensland Museum. Abbreviations: Carapace length (CL) and width (CW), abdomen length (AL) and width (AW). Eyes: anterior median (AME), anterior lateral (ALE), posterior median (PME), posterior lateral (PLE). Spinnerets: anterior (ALS), median (PMS), posterior (PLS); left (l), right (r). Measurements are in millimetres.

SYSTEMATICS

Jamara gen. nov.

DIAGNOSIS

Three clawed cribellate spider less than 1.5mm in length. Posterior row of eyes procurved, anterior row recurved; AME reduced, x0.25 other eyes. ALS widely separated by divided cribellum. The genus is monotypic; type species, *J. pisinna*.

ETYMOLOGY

'Jamara' is the general term for 'spider' in the Ngajan dialect of the Dyirbal language spoken by aborigines from the Upper Russell River region. Specific epithet; Latin; *pisinnus*, small.

Jamara pisinna sp. nov. (Figs 1-3)

TYPE MATERIAL

HOLOTYPE: ♀, Bellenden Ker Range, northeastern Queensland, 17°16'S, 145°51'E, ex moss on tree trunks, 1560m, 25.x-7.xi.1981, Earthwatch/QM Expedition, QMS22777.

PARATYPES: 5♀,♂, same data as holotype, QMS22778; 4♀, QMS22779; ♂, QMS22780; ♀, Mt Bartle Frere, 0.5km N of South Peak, 17°24'S, 145°59'E, 1500m, 6-8.xi.1981, Earthwatch/QM Expedition, QMS22781. OTHER MATERIAL: detached ♀ epigynum, ♂ palp, same data as holotype, QMS22782.

DIAGNOSIS

Long, coiled insemination duct. Large, non-membraneous conductor, very long spiniform embolus. Large, branched median apophysis, tibial apophysis branched with a small ventro-retrolateral branch with spines and a very long pointed dorso-retrolateral branch.

DESCRIPTION

Carapace light brown; dorsal abdomen with dark uniform pattern or pale with darker chevron pattern posteriorly (Fig. 1A); ventral abdomen pale. Clypeus more than diameter of AME (Fig. 1B). Sternum as long as wide, truncate posteriorly. Serrula on endite. Labium wider than long (Fig. 2B). Chelicera with two retromarginal and two promarginal teeth; two frontal setae on chelicera; long promarginal filamentous seta at base of fang. Legs 1=423; trochanters unnotched. One long proximal trichobothrium on tarsi, two shorter trichobothria on metatarsi. Bothrium collariform (Fig. 2A). Small, almost circular, tarsal organ (Fig. 2A), mid-way along tarsus. Abdomen oval. Anterior spinnerets largest (Fig. 1D).

Female: CL 0.5, CW 0.4, AL 0.6, AW 0.5. Ratio of AME: ALE: PME: PLE is 1:4:4:4 (Fig.

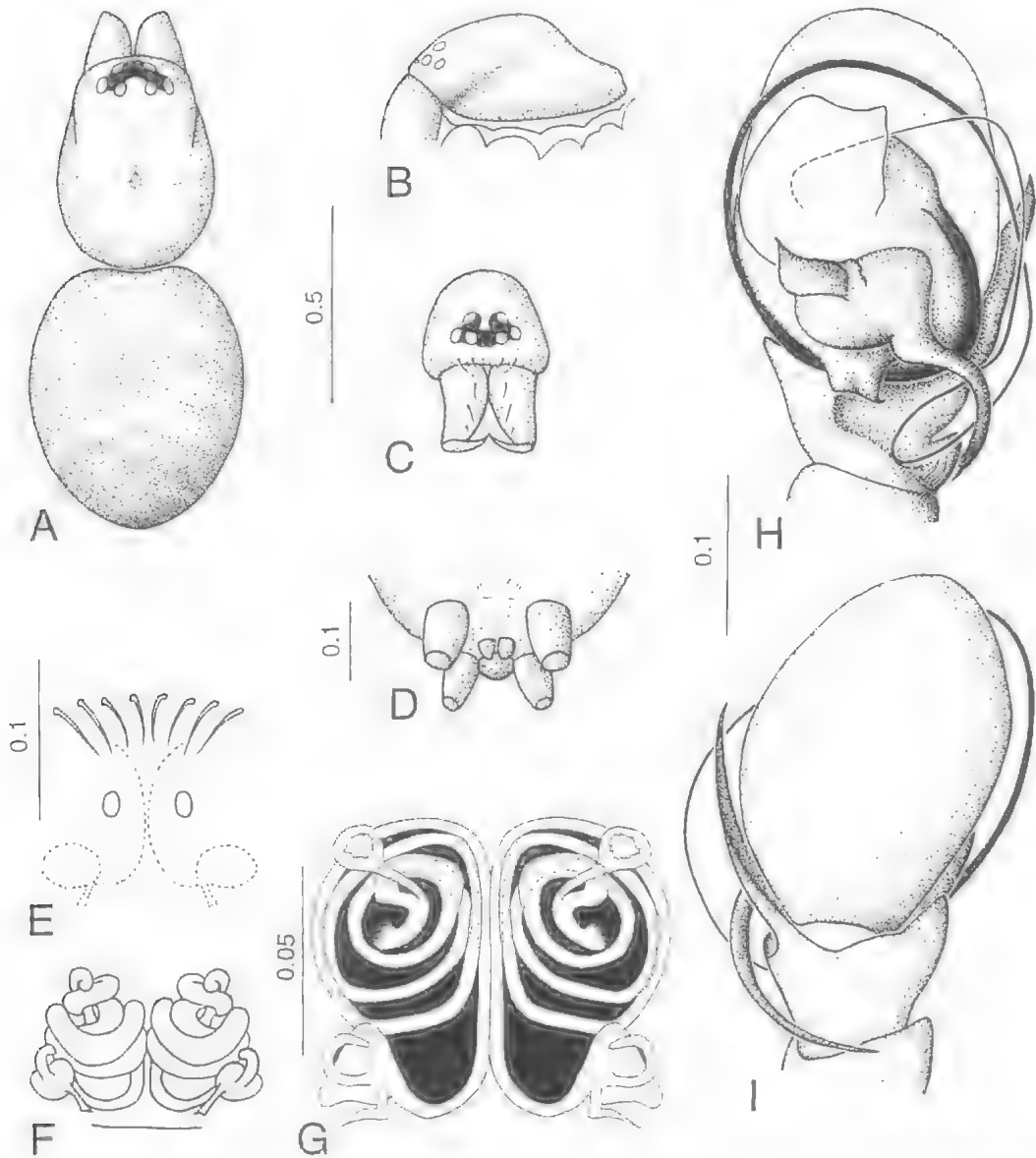


FIG. 1. A-I, *Jamara pisinna*. A, ♀ dorsal. B, cephalothorax, lateral. C, eyes and chelicerae, frontal. D, spinnerets, ventral. E-G, epigynum, ventral, dorsal, dorsal (compound microscope). H, I, ♂ palp, ventral, dorsal.

1C). Frontal setae on chelicerae slightly enlarged. Leg lengths (femur-tarsus): I and IV (0.9), II (0.8), III (0.7). Notation of spines: Ventral tibial and metatarsal spines not enlarged cf *Midgee* (Davies, 1995). Femora: I, D010, V021; II, D010, V111; III, D010; IV, D110, V011. Tibiae: I, V220; II, V220.

Divided cribellum (Fig. 3A), 5-6 calamistrall setae on proximal metatarsus IV. ALS with one major ampullate spigot and 3-4 piriform spigots

(Fig. 3C). PMS with 4 spigots, one large posterior spigot (? minor ampullate) and 3 anterior spigots, larger one (cylindrical) and 2 smaller aciniiform spigots (Fig. 3E). PLS with 3-4 spigots (Fig. 3G). Epigynum (Fig. 1E-G). Long coiled insemination ducts with accessory gland leading to small posterior spermatheca with diverticulum.

Male: CL 0.5, CW 0.4, AL 0.6, AW 0.4. Leg lengths: I and IV (1.1), II (0.9), III (0.8). Eyes, spines on legs, similar to female. Large colusus

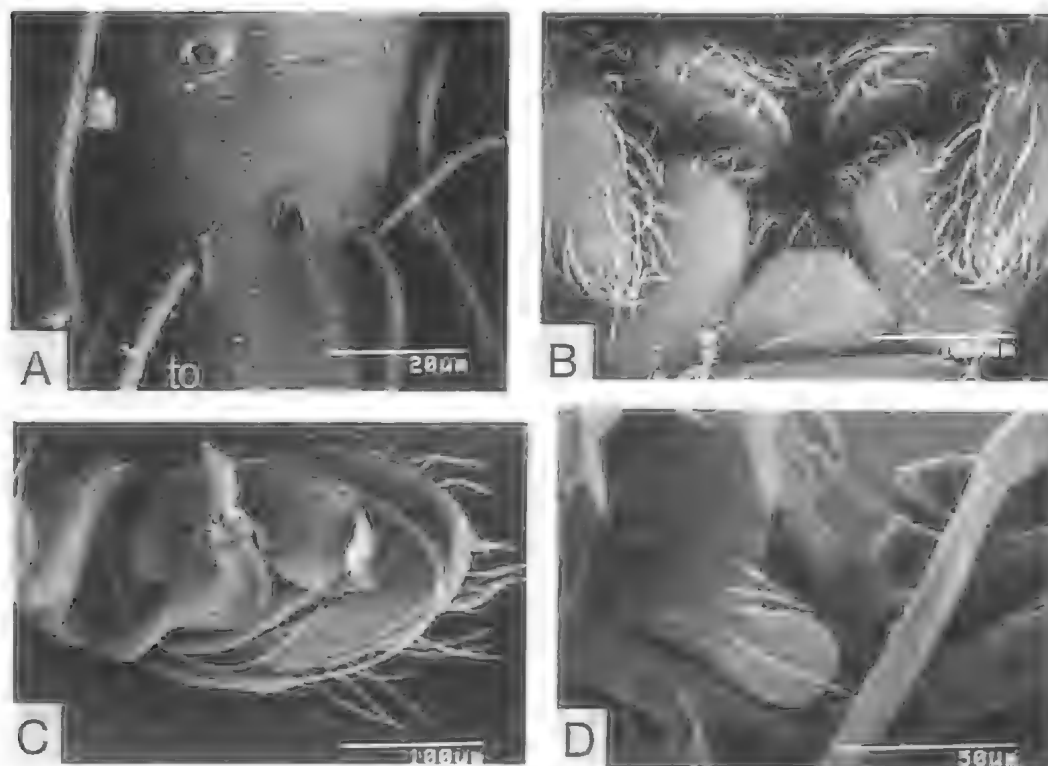


FIG. 2. A-D, *Jamara pisinna*. A, ♂ tarsus 1, bothrium, tarsal organ (to). B, ♀ chelicerae, endites, labium. C, ♂ palp, ventral. D, tibial apophysis base, retrolateral.

(Fig. 3B). ALS with one major ampullate and 3 piriform spigots (Fig. 3D). PLS with one aciniform spigot (Fig. 3H). PMS with one (minor ampullate) spigot only (Fig. 3F). ♂ palp (Figs 1H, 2C): spiniform embolus arising retrolaterally, encircling tegulum then turning back on itself to lie dorsal to the large conductor. Median apophysis with short prolateral branch and long pointed retrolateral branch curving round tibia to dorsal surface (Fig. 1I). Tibial apophysis with small blunt spined branch (Fig. 2D) and long pointed dorso-retrolateral branch reaching half-way up the cymbium.

REMARKS

Cribellate *Jamara* is closely related to ecribellate *Midgee* (Davies, 1995). Its web is unknown but is likely to be a small sheet web in the moss. *Jamara* differs from *Midgee* in having a cribellum, longer insemination duct and embolus, a prolateral branch of median apophysis and in lacking the enlarged tibial and metatarsal spines on legs I, II. The widely spaced anterior spinnerets, procurved posterior row of eyes, the large

non-membraneous conductor arising anteriorly on the tegulum and the spined ventro-retrolateral branch of the tibial apophysis are the apomorphies for the midgeeines. I consider the group *incertae sedis* within the Amaurobioidea.

ACKNOWLEDGEMENTS

I thank Earthwatch and the Centre for Field Research, Boston, Mass. for supporting field work in 1981 and the Council of the ABRS for funding illustrator C. Lambkin; the Wet Tropics Management Agency for support of SEM work by Kylie Stumkat. I thank Professor R.M.W. Dixon, linguist, A.N.U for suggesting the name. Thanks to staff of the Queensland Museum particularly Jennifer Mahoney for help in manuscript preparation.

LITERATURE CITED

- DAVIES, V.T. 1995. A tiny litter spider (Araneae: Amaurobioidea) from Australian rainforests. Records of the West Australian Museum, supplement 52:119-129.

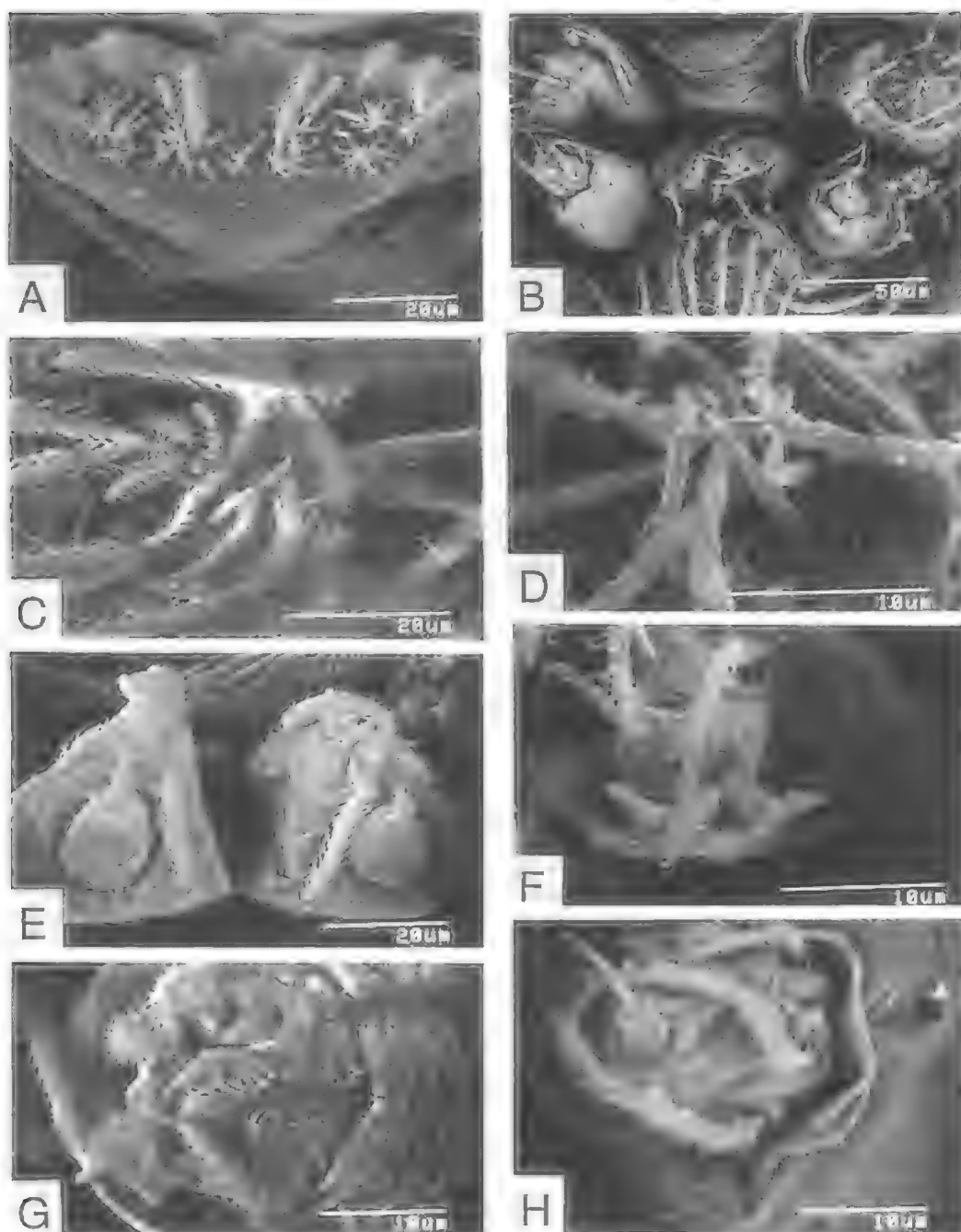


FIG.3. A-H, *Jamara pisinna*. A, ♀ cribellum. B, ♂ colulus, spinnerets, anal tubercle. C, ♀ ALS (l). D, ♂ ALS (l). E, ♀ PMS. F, ♂ PMS (l). G, ♀ PLS (r). H, ♂ PLS (r).

MONTEITH, G.B. & DAVIES, V.T. 1991. Preliminary account of a survey of Arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pp. 345-364. In Werren, G. & Kershaw, P. (eds), 'The rainforest legacy: Aus-

tralian national rainforests study', 2. (Australian Government Printing Service: Canberra).

PLATNICK, N.I. & SHADAB, M.U. 1975. A revision of the spider genus *Gnaphosa* (Araneae, Gnaphosidae) in America. Bulletin of the American Museum of Natural History 155: 1-66.

A NEW OSTEOLEPIFORM FISH FROM THE LOWER CARBONIFEROUS RAYMOND FORMATION, DRUMMOND BASIN, QUEENSLAND

RICHARD C. FOX, KENTON S.W. CAMPBELL, RICHARD E. BARWICK & JOHN A. LONG

Fox, R.C., Campbell, K.S.W., Barwick, R.E. & Long, J.A. A new osteolepiform fish from the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland. *Memoirs of the Queensland Museum* 38(1): 97-221. Brisbane. ISSN 0079-8835.

Cladarosymblema narrienense gen. et sp. nov. (Megalichthyidae, Osteolepiformes), herein described from the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland, Australia, is the first megalichthyid described from the Southern Hemisphere. The holotype of *C. narrienense* is preserved in siltstone and is a crushed specimen with skull, mandibles and anterior postcranial elements still together. Paratypes are isolated parts of the skeleton which have been etched with acetic or monochloroacetic acid from limestone immediately underlying the siltstone. As a consequence of the detail preserved in these specimens, *C. narrienense* is the best known member of the Megalichthyidae. The sedimentary unit in which the fossils are preserved was probably deposited on a floodplain, in a semi-persistent lagoon which supported abundant calcareous algae and a rich fauna of actinopterygians, acanthodians and crossopterygians. This standing body of water was subject to occasional flooding during which penecontemporaneous sedimentary clasts were washed in, along with silt and sand. The family Megalichthyidae is herein redefined using skull, mandible, pectoral girdle, pectoral fin, and axial ring characters, giving a much broader definition than has been used previously. We include *Megalichthys*, *Ectosteorhachis*, *Cladarosymblema*, an unnamed new genus from Norway and an unnamed species from Turkey. Attention is drawn to great variability of the bone pattern in the roof of the rostral region of the skull in *C. narrienense*. The use of such bone patterns for the diagnoses of genera without a knowledge of their variation in the component species, is questioned. Lateral line canals in the rostral region of *C. narrienense* are discussed, and they are shown to be separated from the ossification centres of some of the bones through which they pass, in some instances lying along the sutures between bones. The significance of these observations for the definition of bones in the nasal and postrostral series is pointed out. Braincase structure of both ethmoid and otico-occipital units, the hyomandibular, and the neural and vascular systems of the mandible of *C. narrienense* are described and figured. More detailed information on the hyomandibular is available than for any other osteolepiform genus apart from *Gogonasmus*; the hyomandibular of that genus is described for the first time. The maxilla has an oblique anterodorsal flange that formed the posterior margin of the choana. A similar structure is described from *Gogonasmus*, already known to be choanate. This condition was probably primitive for osteolepiforms. Other aspects of *Gogonasmus* are described using a new specimen, providing a more secure base for comparison of *Cladarosymblema* with other osteolepiforms. Scale histology and growth of the scales are discussed, particularly in relation to the resorption, deposition and function of cosmine. *C. narrienense* was an elongate animal, that had a mid-body section forming an ellipse with vertical axis slightly the longer, and a slightly more depressed anterior section; this, together with its scale structure, pectoral fin pattern, posteriorly placed median fins, and mouth and dentition, indicate that it was a predatory feeder with subcarangiform locomotion. □ *Megalichthyidae*, *Osteolepiformes*, *Cladarosymblema* gen. nov., Carboniferous, cranial morphology, Raymond Formation.

Richard C. Fox, Laboratory for Vertebrate Paleontology, Departments of Geology and Biological Sciences, University of Alberta, Edmonton T6G 2E9, Canada; Kenton S.W. Campbell & Richard E. Barwick, Geology Department, Australian National University, Canberra, A.C.T. 2601, Australia; John A. Long, Western Australian Museum, Perth, Western Australia 6000, Australia.

Fossil fish have been known from the Drummond Basin (Fig. 1) since Smith (*in* Jack & Etheridge, 1892) reported scales in railway cuttings west of Bogantungan, Queensland. Although attempts were made by geologists from government instrumentalities, oil companies and

universities to collect suitable material for description, adequate collections were never assembled.

In 1966, de Bretizel, a geologist with Aquitaine Petroleum Ltd., reported specimens *in situ* in the Telemon and Raymond formations and sent a

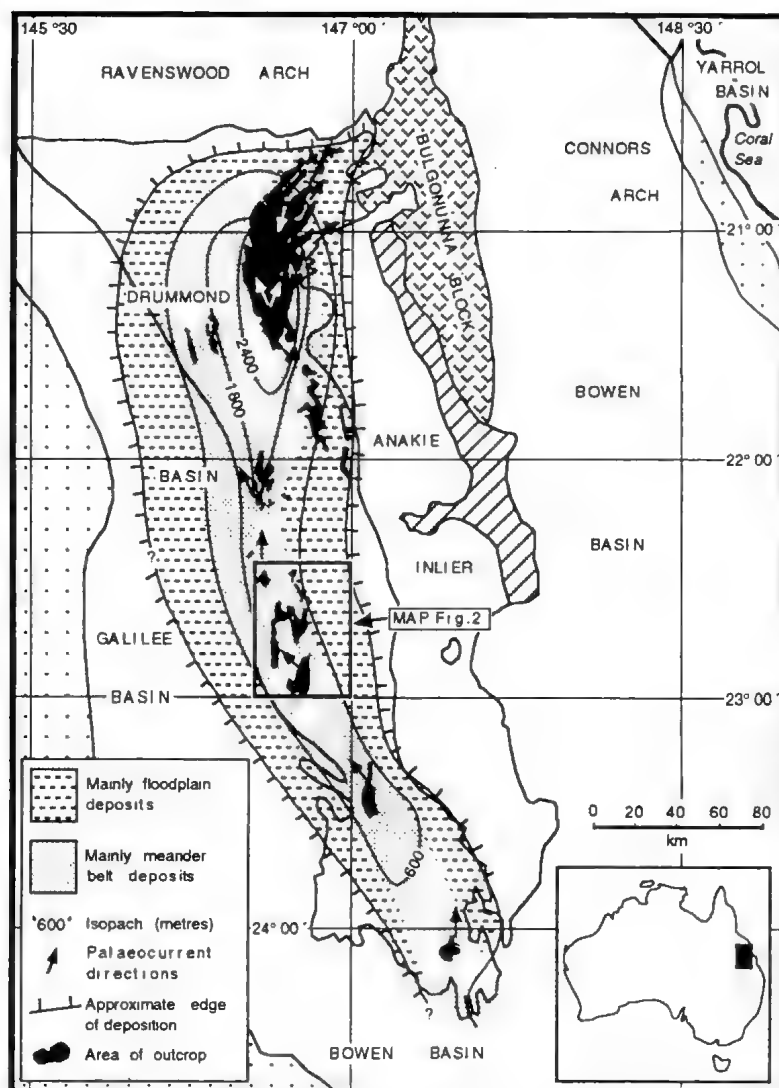


FIG. 1. Map showing the position of the Drummond Basin and its relationship to surrounding tectonic units, and the areas of outcrop, isopachs, and directions of sediment transport of the Raymond Formation. The area covered by Fig. 2 is shown by a rectangle. (Modified from Olgers, 1972).

limestone block full of fish remains, that was collected along a roadside, to the Queensland Museum. Dr Susan Turner of the Queensland Museum made collecting trips to the Narrien Anticline in 1984-5 and found a new fish locality in the Telemon Formation. In 1986, Long prepared a manuscript on the specimens collected by de Bretzel and Turner, but this was never published because he realised that the species involved may have been represented by more

adequate material from the Raymond Formation and was also doubtful about the provenance of the de Bretzel specimen. We here provide a description of that material and compare it with our better localised and more adequate sample. In the same year Long and Arvid Buskas, a postgraduate student at the ANU, located the bed from which the present material has been collected. This had been visited previously by Dr Turner. The collection studied in the present work has been made by Long and Buskas, and by Fox, Barwick, Campbell and William Ellis, a student assistant, in 1986; and Barwick and Campbell in 1990. All the specimens of *Cladarosymblema narrienense* described herein, except the holotype, have been etched from more than 500 kg of limestone from a single stratum.

The fish fauna from the above locality, which we will refer to as the Police Mountain Track locality (Fig. 2), consists of at least five fish species - one crossopterygian, three actinopterygians and one acanthodian. Long found numerous acanthodian specimens in the de Bretzel block, suggesting that it did not come from our locality. In addition to the specimens definitely identified as fish,

we have found a few large postcranial bones that are large enough to be amphibian but are possibly rhizodontiforms. At present we have too few of these to warrant description.

Herein we describe from the Raymond Formation one osteolepiform fish, with which we compare the osteolepiform fish from de Bretzel's material. Long (1986) has described some of the acanthodians from the de Bretzel limestone

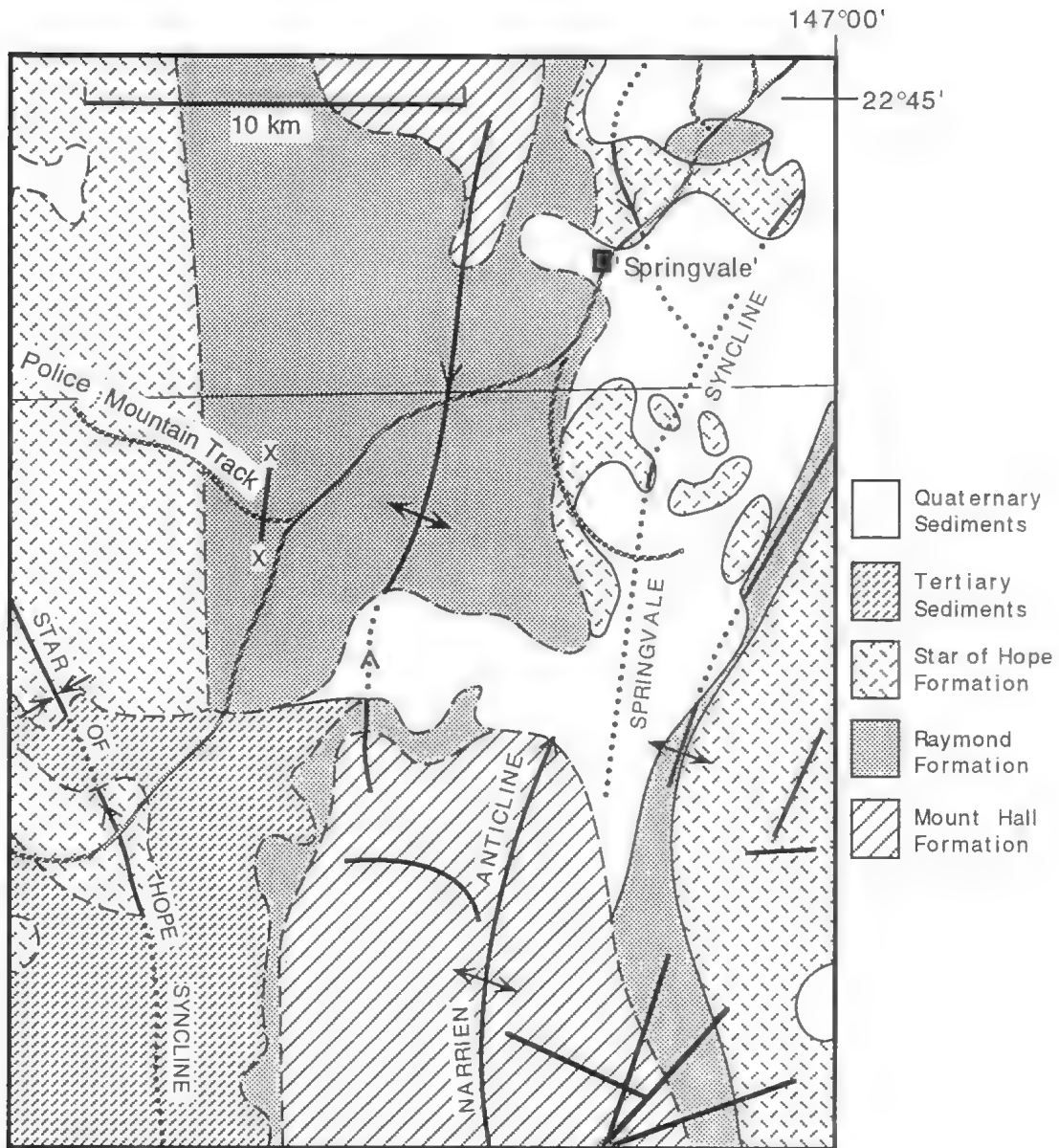


FIG. 2. Generalised geological map of the Springvale area from which the material described was collected. Position of collecting localities shown thus: X—X. (Modified from Vine & Douch, 1972.)

block, and the other osteichthyans will be the subject of another paper.

Osteolepiforms known from the Devonian of Australia include *Gyroptychius australis* Young & Gorter from the Middle Devonian rocks at Burrinjuck Dam, N.S.W., *Gogonasus andrewsae* (nom. corr. for *G. andrewsi* Long) Long from the Frasnian of the Canning Basin, W.A., and *Marsdenichthys longioccipitus* Long and

Beelarongia patrichae Long from the Frasnian of Mt. Howitt, Victoria. The problematical *Canowindra grossi* Thomson from the Upper Devonian of New South Wales has been regarded as an osteolepiform by Long (1985b,c) and by Young et al. (1992). The new genus is the first occurrence of a well-preserved osteolepiform from the Australian Carboniferous. The only other crossopterygian fish described from the Carbonifer-

ous of Australia is the rhizodontid *Barameda decipiens* from redbeds near Mansfield, Victoria (Long, 1989). This dearth of crossopterygians is surprising in view of the large number of fishes obtained from the Gogo Formation, and the great thickness of suitable sediments of Devonian and Carboniferous age in all the eastern States. The occurrences reported from both the Telemon and Raymond formations suggest that an aggressive search of the Drummond Basin will produce more freshwater genera, and Long's discovery of rhipidistian fish remains in the Carboniferous rocks of the Canning Basin of Western Australia suggest that more marine genera will turn up there.

STRATIGRAPHY AND ENVIRONMENT

Specimens described herein were obtained from a carbonate bed in the Early Carboniferous Raymond Formation, which crops out extensively in the Drummond Basin (Fig. 1). The fossil bed is exposed on the eastern flank of a small, local anticline whose axis is offset from that of the larger Narrien Anticline and lies west of the Springvale Syncline (Vine & Douth, 1972; see also Fig. 2). These structures lie about the mid-length of the meridionally oriented Drummond Basin.

The Drummond Basin is an intracontinental structure formed during the Late Devonian and Carboniferous west of the Anakie High in central Queensland. Sediments within it locally overlie the Upper Devonian Silver Hills Volcanics and were deposited in fluvial and lacustrine environments. Sediment transport throughout its history was south to north. As would be expected, the sediments consist mainly of conglomerates, sandstones and shales, all of which show rapid lateral facies changes. The stratigraphic column shown in Fig. 3 has been drawn up from the northern part of the basin where the thickness is greatest. The fossil locality is about 150km to the south of this depocentre, where the thickness is approximately three quarters of the maximum further north. The rate of sediment accumulation was enormous, the Lower Carboniferous sequence being measured at 12 000m thick (Olgers, 1972).

The nearest contemporaneous sea was either to the north of the Lolworth-Ravenswood Arch, or at the northern end of the Yarrol Basin, even if allowance is made for the westward translation of that structure in post-Carboniferous times. In both of these areas, Early Carboniferous brachio-

| AGE | NORTHERN DRUMMOND BASIN | | |
|--------------------------------------|---|------------------|---|
| | Formation | Max. Thick. in m | Lithology |
| LATEST CARBONIFEROUS & YOUNGER | GALILEE BASIN SEQUENCE & BULGONUNNA VOLCANICS | - | |
| EARLY CARBONIFEROUS | NATAL FORMATION | 1200 | Quartzose and feldspathic sandstone, siltstone and mudstone |
| | * BULLIWALLAH FORMATION | 1800 | Lithic and feldspathic sandstone, with minor siltstone, mudstone and tuff |
| | STAR OF HOPE FORMATION | 1800 | Varicoloured tuff, sandstone, conglomerate and siltstone |
| | RAYMOND FORMATION | 1000 | Quartzose sandstone with minor siltstone and mudstone |
| | MOUNT HALL FORMATION | 3000 | Quartzose sandstone and conglomerate Minor lithic sandstone and mudstone |
| LATE DEVONIAN TO EARLY CARBONIFEROUS | # SCARTWATER FORMATION | 1200 | Feldspathic and lithic sandstone, mudstone, tuff and algal limestone |
| | SAINT ANN'S FORMATION | 2100 | Rhyolite, tuff and algal limestone. |
| EARLY AND MIDDLE DEVONIAN | UKALUNDA FORMATION | - | Siltstone, sandstone and limestone; metamorphosed in part |

FIG. 3. Generalised stratigraphic column from the depocentre at the northern end of the Drummond Basin. The entire sequence apart from the Ukalunda Formation consists of volcanic and fluvial or lacustrine deposits. * indicates the position of the Ducabrook Formation, a facies equivalent of the Bulliwallah Formation and the # indicates the position of the Telemon Formation, a facies equivalent of the Scartwater Formation. (Modified from Olgers, 1972.)

pods, corals and molluscs are present. However, no Carboniferous marine fossils are known from the Drummond Basin.

The Raymond Formation was named the Raymond Flaggy Sandstone by Hill (1957), a name reflecting its overall nature. In the vicinity of the fossiliferous bed, the rocks are mainly grey- or buff-coloured sandstones and siltstones that show many evidences of shallow water deposition. Interference ripples, wind-ripple drift, and channels filled with cross-stratified sands are common within or adjacent to the fossil bed, and there are sporadic sand-filled mud cracks. Moreover, mud clast conglomerates, indicating the break-up and erosion of nearby penecontemporaneous sedi-

ments, demonstrate that the water was so shallow that mud cracking and redeposition were features of the environment. Many of the rocks, including those within which the fish are preserved, contain macrofloral remains, usually lepidodendroid stems. These points, in association with the evidence of the sediments and the palaeogeography, indicate that the fish fossils are of freshwater origin.

The carbonate unit can be traced over a distance of approximately 3 km. At its northern extremity the carbonate content gradually decreases; the bed becomes a silty sandstone, containing few fish. At the southern end soil cover obscures the outcrop, but we have been unable to find the bed in the appropriate stratigraphic position further around the structure even where the outcrop improves. Nor have we been able to find it on the other side of the anticline. Consequently, we conclude that the limestone bed was deposited over a restricted area, probably in a restricted environment. It is possible, of course, that the bed was more widely distributed, and was eroded from neighboring areas penecontemporaneously. Because the limestone laterally grades into siltstone at its northern end, and at its southern end it consists of lenticular units, we do not accept that hypothesis.

The fossiliferous limestone is up to about 2 m thick, but it varies considerably in thickness over the outcrop. In its northern half the limestone is persistent, and is commonly 1.0–2.0 m thick. In the southern part of the outcrop the unit is less persistent and is rarely more than 0.5 m thick. It lenses out from 0.5 m to nothing within a few metres along strike, and then reappears equally rapidly. This is interpreted as the result of deposition in isolated patches rather than penecontemporaneous erosion.

In the north, the base of the bed is an algal pellet limestone about 0.5 m thick, which contains few

fish. The remainder of the unit contains abundant fish remains and is composed of carbonate mud containing quantities of terrigenous sand, silt and, in many places, flat mud and silt clasts up to 10 cm in diameter. Despite the abundance of carbonate, no sign of invertebrate remains has been found. Many of the clasts are carbonate rich, consisting of scattered quartz grains in a mud matrix containing carbonate. Some of the clasts are completely overgrown by algae (Fig. 4A) indicating movement before burial, and others are partly coated with algae (Fig. 4E). Presumably this means that these silt and mud clasts were at least slightly hardened and overgrown before transport. Others were still soft when deposited, because their edges are not sharp, but merge into the surrounding matrix, suggesting partial disintegration during deposition. Occasional small clasts are made of algal carbonate (Fig. 4E), and many of these show the coliform external shape of the growing algal colony (Fig. 4A). The finer-grained matrix consists of mud and silt with large amounts of carbonate; and a carbonate cement. Many fine sand-sized clasts are made of angular quartz. Locally abundant bodies that appear in thin sections as sand-sized groups of radially-arranged calcite crystals, are interpreted as *Microcodium*, structures that are formed as the result of the infilling of root spaces during exposure to the atmosphere (Scholle et al., 1983).

Some larger clasts contain fish fragments (Fig. 4D) indicating that the specimens were disaggregated and deposited in the soft silty sediment. This was then dried out and cracked, and the resulting clasts were redeposited. Such an interpretation implies that some of the isolated fish fragments that are now found in the matrix of the rock were reworked from penecontemporaneous sediment. None of the clasts consists of igneous rocks or of earlier Palaeozoic sediments; this

overleaf on pp. 110–111

FIG. 4. A–E, thin sections of sediment from which the fossils have been extracted. All figures have been prepared by printing the thin section in an enlarger. A, QMF31882, section cut normal to bedding. Shard-like bodies are fish scales. Numerous small white spherical bodies are composed of carbonate. The large mass (a) is a clast still showing bedding. Most other clasts are intraclasts. Those labelled (b) are completely coated with algae. Note some of the clasts have clearly defined boundaries, but those labelled (c) merge into surrounding matrix or show highly irregular boundaries indicating that they were soft when deposited. Cloud-like bodies (d) are algal growths; some are attached to clasts, others have broken free. (e) section through a cartilage bone. B, QMF31883, section parallel with bedding. Most sharp-edged fragments are scales; silty matrix is largely carbonate. C, QMF31884, section normal to bedding; shard-like bodies are scales; dark oolite-like bodies are teeth, appearing as circles demonstrating that they were current-oriented. Note clast (a) has been squeezed out laterally during compaction, indicating that it was soft when deposited. D, QMF31885, section normal to bedding showing large clasts separated by carbonate silt with many fish fragments. Clast (a) itself has an embedded fish fragment; its right margin merges into the matrix. E, QMF31886, section normal to bedding. Upper side of flat clast (a) is encrusted with algae; several well-defined algal balls (b) are present. Scales: 10 mm.

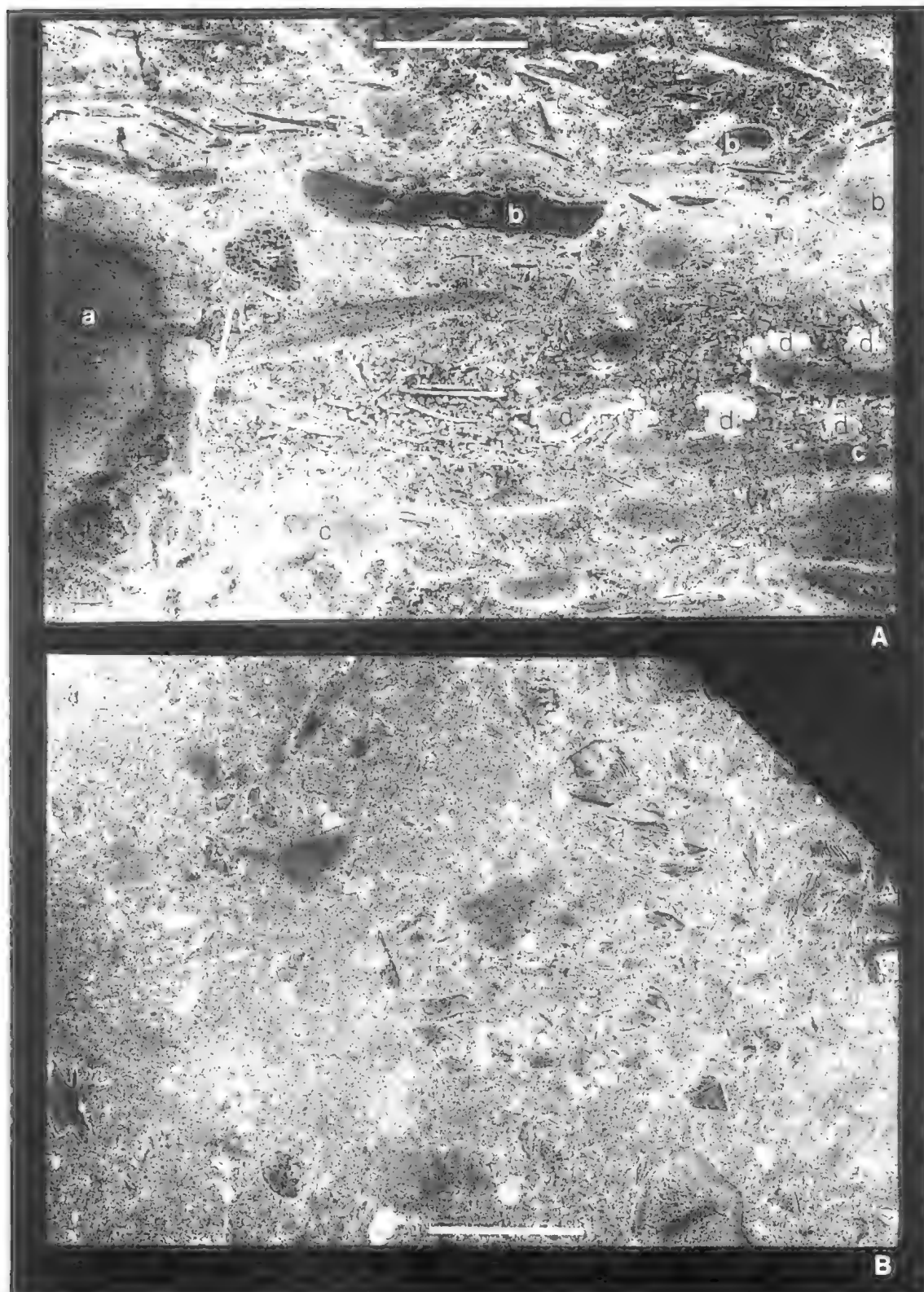


FIG. 4A, B.

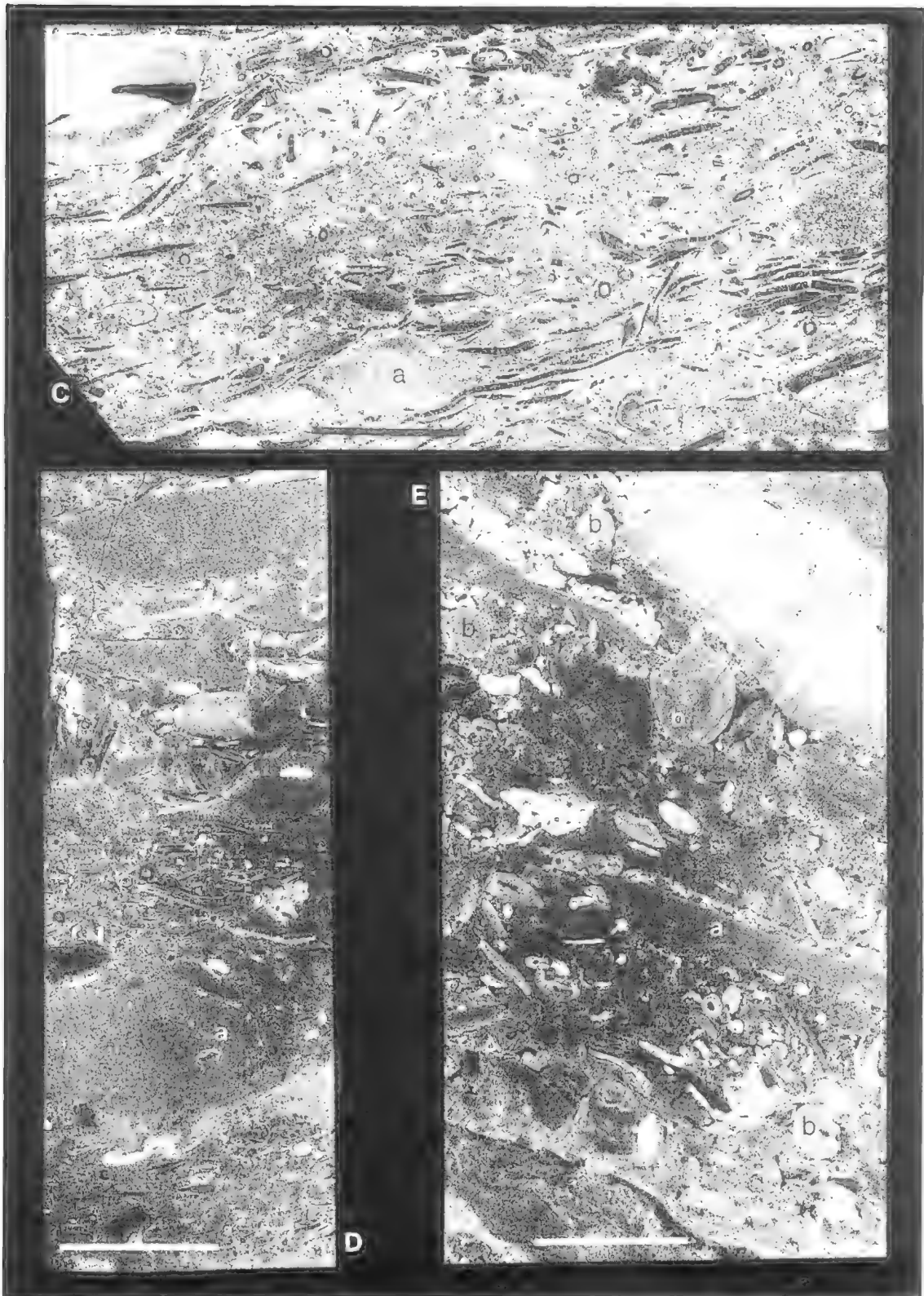


FIG. 4C-E.

indicates that no distant transport was involved, and that any currents were of short duration.

Fish remains, whether scales or cranial plates, almost all lie parallel with the bedding, which they help to define in hand specimen (Fig. 4A,C). In thin section many have uniform, small diameter tubes that are now filled with chemically-deposited carbonate. These are of appropriate size and shape to be borings made by either algal hyphae or nematodes. Absence of imbrication indicates low velocity depositing currents. Several well-formed coprolites, cylindrical in form, have been recovered from the etches. These would not have been preserved if they had been subjected to much movement on the bottom. Of course, the nature of the sedimentary clasts also precludes strong persistent currents. We conclude, therefore, that periods of excess energy disrupting bottom sediments were short-lived but rapidly broke up skeletons and caused unconsolidated mud to infiltrate main skeletal cavities.

Sandier units within the limestone are commonly cross-stratified. In places, channels subsequently filled with coarse sediment cause slight thickening of the unit. These channels were cut in the underlying sediments and filled with carbonate and terrigenous clasts.

We interpret the depositional environment as a semi-persistent lagoon formed by a body of overbank water in which freshwater calcareous algae grew, and fish were able to make permanent habitations. During floods, water flowed through and around the lagoon disrupting the carbonate-rich sediments and transporting clasts torn up from the surrounding, recently deposited, sediments. The abundance of *Microcodium* in some sections indicates that plants were growing on the adjacent sediment or perhaps actually on the carbonate itself. On occasions new temporary channels were established, and conglomerates were formed in these.

The fish are almost always fragmentary, and it is uncommon to find whole otico-occipital or ethmoid units. Scales are scattered through the whole deposit. Only one assembled specimen, the holotype, was found, and it was lying in a siltstone/sandstone layer immediately on top of the limestone. Specimens preserved in three dimensions are filled with carbonate mud; none have a crystalline calcite infill. It is concluded that the skeletons were disaggregated before interstitial carbonate precipitation could occur.

As a result of this mud infilling, sediment compaction has resulted in cracking and disruption of

most specimens. This is unlike the fish from the Gogo Formation, Western Australia, where crystallisation of carbonate in the open spaces within and between bones took place during early diagenesis, preventing skeletons from crushing. Most flat specimens of *Cladarosymblema*, such as the roofing bones and operculars, are badly cracked and fall apart during etching. Despite disaggregation, few bones show evidence of abrasion, indicating little transport.

The Drummond Basin is analogous tectonically to the Lambie Basins of New South Wales and Victoria, which are predominantly filled with Upper Devonian redbeds, and contain thick sequences of conglomerates, which, although concentrated near the base of the sequences, occur at many levels. At many horizons freshwater algal pellets are very common, and placoderms are frequently found in such sediments. However, we note that the Drummond sediments include fewer redbeds, and conglomerates are not concentrated in the basal formations. In our opinion, this is not the result of a different tectonic environment, but rather of a wetter climate. Such an interpretation would account for the persistent standing body of water that would be necessary to account for the limestone in which *Cladarosymblema* is found.

AGE OF THE RAYMOND FORMATION

In the absence of marine fossils or volcanic rocks from which radiometric dates could be obtained, spores, plant macrofossils and microvertebrates provide the only means for dating this formation. Only a limited number of palynological determinations have been made on sediments from the Drummond Basin, and all of these were by Dr Geoffrey Playford. The palynostratigraphy was reviewed by Kemp et al. (1977) and Playford (1985). The plant macrofossils have been studied by White (1972).

Lepidodendroids are the common plants in the sequence. *Leptophloeum australe* (McCoy) is common in the Late Devonian of eastern Australia, but has never been recorded above the earliest Tournaisian (Jones et al., 1973). In the Drummond Basin, it is not recorded in beds higher than the Mt. Wyatt Formation, which overlies the Lower Devonian Ukalunda Formation and unconformably underlies the Drummond Group in the extreme north of the basin. It is separated from the Raymond Formation by several thousand metres of sediment. Other species of lepidodendroids occur in all the formations between it and the Raymond Formation. The

common species in the Raymond Formation is the long-ranging Carboniferous species *Lepidodendron veltheimianum* Sternberg, which occurs through several formations above and below. The exclusively Carboniferous *Rhacopteris digitata* Etheridge fil. also enters the sequence several thousands of metres below the Raymond Formation, but above the Mt. Wyatt Formation. We conclude that the macroflora gives no more precise age for the Raymond Formation than some level above the base of the Carboniferous.

Playford (1976, 1977) described spores from the Ducabrook Formation, which is higher in the sequence than the Raymond Formation, and has assigned them to his *Anapiculatisporites largus* Assemblage. He considered this assemblage to be of late Viséan age for two reasons: 1, the same assemblage occurs in the Tanmurra Formation and the upper Bonaparte Beds of the Bonaparte Basin, Western Australia, where it is dated by marine invertebrates; and 2, some species of palynomorphs from the assemblage are known elsewhere only from the late Viséan of Britain. Playford (1985), in the most recently published review of Australian Lower Carboniferous palynology, showed the Raymond Formation as late Tournaisian in age, not because he had additional information, but because he spaced the formations between the *Leptophloeum australe* Flora and the *Anapiculatisporites largus* Microflora. Thus the macrofloras indicate that the formation is probably younger than Tournaisian, and the microfloras show that it cannot be late Viséan or younger.

Samples of the fish-bearing rock have been etched by Dr Clinton Forster of the Australian Geological Survey Organisation with a view to studying palynomorphs, but no identifiable short-ranging spores have been recognised.

Turner (1993) studied the microvertebrates of the Raymond Formation at the site from which our material comes. Although there is no precise identity between the Raymond Formation species and those from elsewhere in the world, she considered it possible to draw general conclusions about the age and environment of deposition of the formation. In her opinion the fauna is early to middle Viséan in age, although the control is limited by the range of data available. She further considered that the fish fauna has elements in common with the Scottish Viséan, an interesting point in view of the presence of megalichthyids in the same region. This is slightly younger than suggested by Playford, but is within the range

indicated by plant data. We conclude that the most reliable age estimate available at present is early to middle Viséan, an age consistent with the occurrence of megalichthyids.

MATERIALS AND METHODS

The amount of carbonate cement and matrix can be judged from the mode of preparation we have had to adopt. Each specimen underwent many cycles of immersion in acid for up to seven days, washing for two or three days, drying over a period of days, and finally impregnating with dilute plastic. The matrix does not completely disaggregate under acid treatment, but the rock becomes soft and is easily removed by scraping and/or brushing with a soft hair brush. Many specimens have required immersion and impregnation as many as thirty times.

The specimens were all whitened with ammonium chloride before being photographed. The specimens examined by scanning electron microscope were gold-coated.

The holotype is the only specimen prepared mechanically, and that was done by vibrotool and needle.

Materials cited in this work are registered with the Queensland Museum (QMF), Western Australian Museum (WAM), Australian National University Geology Department (ANU), Royal Ontario Museum (ROM), British Museum Natural History (BMNH), Hancock Museum, Newcastle-on-Tyne (G) and Hunterian Museum, Glasgow (V).

TERMINOLOGY

ETHMOID UNIT: the part of the skull anterior to the intracranial joint, including the skull roof and endocranium of that part of the skull.

OTICO-OCCIPITAL UNIT: the part of the skull posterior to the intracranial joint. As with the ethmoid unit, it includes the skull roof and the endocranium.

NOMENCLATURE OF SKULL ROOFING BONES: We do not wish to become involved in discussion of this matter, as our purpose is to describe a new genus and indicate its relationships with other osteolepiforms. We have chosen the terminology of Westoll (1936), Romer (1937) and several later authors, most recently Ahlberg (1991), which is based on comparison with primitive tetrapods. The matter has been extensively discussed by Borgen (1983).

We wish to comment, however, on the nomenclature of the nasal, rostral and tectal series. Definition of the nasals depends on the presence of

lateral line canals within them, and the other two series lie mesial and lateral to the nasals respectively. Our observations of the snout of *Cladarosymblema* indicate that the position of the lateral line canal is sometimes not clear from observations of the external surface, particularly if reliance is placed on lateral line pores. It is necessary to work from X-radiographs, excavated canals or specially prepared internal surfaces. Even when this is done, it is found that in some specimens the canals run along the sutures between bones in some places, around the centres of ossification in others, and through the centres in yet others. Consequently the identification of the nasal series is sometimes ambiguous. Hence identification of rostrals and tectals is sometimes uncertain. We are wary of some statements in the literature concerning these bones, and advise caution in recognising taxa on the basis of such criteria. A second point concerns the difference in the arrangement of bones of these series on opposite sides of the one specimen. There seems to be little point in trying to homologise individual bones within these series. The taxonomic value of such an exercise is questionable.

PREMAXILLA: Jarvik (1942:346) stated that the infraorbital lateral line canal 'along the ethmoidal region pierces a paired row of bones, the rostrals, in all three main crossopterygian groups'. In osteolepiforms the toothbearing bone around the edge of the mouth also carries the lateral line. Jarvik therefore referred to it as a compound bone, the rostro-premaxilla, except in species in which he considered that the first nasal was also incorporated. For such forms he used the name naso-rostro-premaxilla. Jarvik claimed to be able to show that in some specimens of *Eusthenopteron* the premaxilla is an independent bone sutured against the rostrals. In all our specimens of *Cladarosymblema* the tooth-bearing bone is large and has a projection extending over the area that is covered by the first nasal bone in such genera as *Osteolepis*. However, the bone in question has a single centre of ossification; hence we have no observable evidence of fusion. We prefer to refer to it as the premaxilla.

PRENASAL FOSSA: Jarvik (1966: figs 17 et seq.) referred to deep fossae roofed with thin endocranial bone and lying anteromesially to the nasal cavities, as 'divisio prenasalis communis of the neural endocranium'. In a complicated terminology of this region, he also used the terms prenasal pit, intervomerine pit and anterior palatal fenestra. We are unable to discriminate detail of this sort on our specimens. In addition, Jarvik has

used the structures he recognised to imply relationships that have not been accorded general agreement. Hence, to avoid confusion, we have not accepted his terminology. The two deep, sub-hemispherical depressions in the endocranium that are clearly separated by a broad median ridge of endochondral bone which is slightly overlapped anteriorly by the posterior process of the premaxilla, are given the non-committal name of 'prenasal fossae'.

SYSTEMATIC PALAEONTOLOGY

Order OSTEOLEPIFORMES Jarvik, 1942

REMARKS

The possibility of defining this taxon has been disputed by Rosen et al. (1981), who considered that it was paraphyletic. Long (1985b,c, 1988, 1989) and Panchen & Smithson (1987), working within a cladistic framework, are among the few who have continued to take this work seriously, and even they have contested its conclusions. Restricting the families included in the taxon to the Osteolepididae and the Eusthenopteridae as then understood, Long claimed that the Osteolepiformes are unique in having a small vertical preopercular, seven bones forming the cheek with the lachrymal as large as the jugal, a dermal shoulder girdle with an exposed anocleithrum, and scutes at the bases of the fins. Panchen & Smithson (1987: 358-362) independently considered that the seven cheek bones were autapomorphic for the Osteolepiformes. In addition, they accepted the presence of scutes at the base of median and paired fins, and a single external naris, from the list provided by Andrews (1973). This composite list of disparate characters does not commend itself to some of us as the basis for the recognition of a major taxon. In our view, osteolepiform and rhizodontiform genera should be analysed in terms of functional systems before an adequate classification is possible, but we do not have access to a complete range of characters that can be interpreted functionally (but see below). Hence we do not attempt the definition of taxa at the level of the Osteolepiformes. On the other hand, we consider the Megalichthyidae to be closer to the Osteolepididae than to any other family, and so we classify them under the order Osteolepiformes simply to indicate that point. We note, however, that the Megalichthyidae falls within the definition of the Osteolepiformes as defined by Long (1985b).

Family MEGALICHTHYIDAE Hay, 1902

DIAGNOSIS

Skull low and wide; no pineal opening; anterior narial opening slit-like, embraced in front by lateral rostral and behind by anterior tectal bones; separate bones dorsal and ventral of this opening absent; maxilla high, with its highest point posterior, leaving only a short edge for junction with the squamosal; outline of squamosal approximately equidimensional; preopercular short and standing vertically. Opercular large, subquadrate in outline, with a H/L ratio of approximately 1; two suboperculars, (see discussion of operculars below), both abutting posteriormost submandibular; subopercular 1 only half the size of opercular; lateral extrascapulars wide. Posterior endocranial wall of trigeminofacialis chamber approximately transverse (see REMARKS below). Tusk on premaxilla positioned behind variably developed row of small teeth; posterior process on premaxilla lying on endocranial palatal lamina of ethmoid shield; prenasal fossa divided by endocranial bone partly covered by posterior process of premaxilla. Vomer transverse in outline, lacking posterior process, but with mesial process meeting, or almost meeting, its fellow in midline. Well-developed, deep anterior mandibular fossa; strong postglenoid process; strong symphyseal tusk on dentary, and teeth reduced or absent in front of it. Scales rhombic but lacking peg-and-socket articulation. Scapulocoracoid very large, and with extensive attachments to cleithrum. Pectoral fins large and fan-shaped.

REMARKS

The diagnosis has been prepared with a view to differentiating the family from other osteolepiform families, and consequently we have used only those osteolepiform characters that are individually unique, or which form complexes unique to the Megalichthyidae. We are aware that it is possible to find outside the family an odd genus that has one or more of the features listed above as unique. In our view this is not significant: the definition of any higher taxon is likely to include statements about characters that have developed independently in unrelated taxa, i.e., homoplastic characters.

For this reason it is necessary to emphasise character complexes, as illustrated by the following three examples.

(A) We acknowledge that the squamosal of some members of other families is almost

equidimensional in outline and that some others have high maxillae, and that yet others have steeply inclined preoperculars, but these features in megalichthyids inter-relate to make a distinctive cheek.

(B) The outline of the opercular in some members of *Osteolepis macrolepidotus* is similar to that of the megalichthyids (Jarvik, 1948: fig. 41). However, note that the opercular in that species is highly variable, it is small in comparison with that of megalichthyids of similar size, subopercular 1 is of like dimensions to the opercular, and that these two bones sit high on the side of the head with the long axis of the opercular inclined to the long axis of the fish. Although we have no specimens of megalichthyids with the opercular series in position relative to the cheek and the shoulder girdle (but see Borgen's illustration of the cheek and operculars of his new genus [MS]), it is clear that the long axis of the opercular must have been almost horizontal and that it covered a large part of the side of the gill chamber, its ventral edge being at about the level of the mandibular articulation; and that subopercular 1 is small in comparison with the opercular. All these features imply significant differences between megalichthyids and *Osteolepis* in the dynamics of the gill chamber.

(C) The significance of the two bones around the anterior naris is that they are placed anterior and posterior to the opening rather than dorsal and ventral. Although this bald statement is made in isolation, the position of these bones was only achieved by a complex rearrangement of the surrounding bones as compared with other osteolepiforms. Yet the diagnosis contains only terse statements about the positions, shapes and relative sizes of all the bones in question, making it possible to object that individual characters are not unique. This illustrates our previous point that the listing of uninterpreted characters such as is found in standard cladistic analyses is almost valueless.

One feature we have left in the diagnosis is the large, flat, fan-shaped pectoral fins, despite the fact that some osteolepidids, such as *Gyroptichius groenlandicus* (see Jarvik, 1985, fig. 8), have similar fins. *Gyroptichius* is a member of the Osteolepididae, which do not normally have fins of this type. We conclude that *Gyroptichius* has evolved this fin type independently. Thus, although the shape of the pectoral fins cannot be said to be unique to the Megalichthyidae, it is a feature that permits a

separation of most members of the Osteolepididae from the Megalichthyidae.

Some characters have not been found in all the named taxa, but we have included them in the diagnosis because we have reason to believe, on the basis of incomplete evidence, that they are so distributed. Other features have been included although they have not yet been discovered in all the included taxa, because we consider that they are very distinctive in the genera in which they are known, and the probability of their occurrence in taxa with correlated characters is high. For example, with regard to the shape of the vomers we note that although only incomplete bones have been found for *Cladarosymblema narrienense*, the shape of the endocranial surface to which the vomers were attached shows that they were very wide, like those of *Megalichthys*. This shape ties in well with the unusual breadth of the rostral unit, and so it has been included as diagnostic.

Other features that may prove useful when better descriptions become available are as follows: (1) The cheek is apparently short in *Megalichthys*, *Ectosteorhachis*, *Cladarosymblema* and a new genus of megalichthyid from the Permian of Norway being described by Ulf Borgen (Borgen, MS), but details are lacking.

(2) It appears that the squamosal is equidimensional in outline, and from the position of the orbit as inferred from the jugal, the postorbital and the jugal must be more elongate than in other osteolepiforms.

(3) The ornament of the dermal pectoral girdle of both *Cladarosymblema* and *Ectosteorhachis* is distinctive, but *Megalichthys* itself is too poorly known to permit the character to be used diagnostically for the family.

(4) A strong oral lateral line canal branches from the mandibular canal in *Eusthenopteron* and it may be a widespread feature in osteolepiforms, but adequate material has never been prepared. *Cladarosymblema* has no oral canal, and from the absence of pits in the surangular of *Ectosteorhachis* and *Megalichthys*, we conclude that the same applies to those genera also. However, absence of an oral canal may be more widespread than that, and so caution has been exercised in using it as a family character.

(5) In *C. narrienense*, the angle between the olfactory tracts in dorsal view is only about 45°, and the dividing point is behind the mid-length of the ethmoid unit. In fact, the division is so far back that the canal for the optic nerve exits from the side of the olfactory tract instead of from the

wall of the braincase proper. The same arrangement has been described for *Ectosteorhachis nitidus* (Romer, 1937: figs 8, 9). The British *M. hibberti* requires dissecting before the olfactory tract configuration is certain, but we consider that specimen V3040 from the Hunterian Museum, Glasgow, although crushed, suggests a posterior divergence like that described above. Should this prove to be so, it is another feature by which the Megalichthyidae may be distinguished from other osteolepiforms.

(6) In megalichthyids, the gutter around the cosmine cover of the scales usually exposes the vesicular bone that forms the core of the scale, and the overlapped part of the scale is lamellar bone on its inner and outer surfaces. A gutter in which vesicular bone is exposed is also known in *Latvius* (Gross, 1956), but the histology of the whole scale has not been described. The value of this feature requires investigation.

We also note that a feature which has not attracted attention in differentiating the Megalichthyidae, probably because it is so rarely preserved, is the form of the endolymphatic sacs and ducts. The only other osteolepiforms in which these structures are confidently known are *Eusthenopteron foordi* and *Ectosteorhachis nitidus*. As Jarvik (1975) has pointed out, in *E. foordi* the supraotic cavities of the two sides converge mesially in a discrete arch that extends posteriorly over the brain stem and exits from the braincase to form an extension down the spinal cord. Romer (1937) showed that no such arch is present in *Ectosteorhachis nitidus*, which has a relatively flat-topped sac without a vertebral extension. Our observations of *Cladarosymblema narrienense* (see below) indicate a different pattern from that of *E. nitidus*. We still lack detail for this region in *Megalichthys hibberti*, detail that can be obtained only by dissecting an appropriately preserved specimen.

Unusual features of *Cladarosymblema* are the large lateral extrascapulars and post-temporals. We have not been able to confirm the presence of similar bones in *Megalichthys*, *Ectosteorhachis* or Borgen's new genus. Borgen, however, has figured a specimen of *M. hibberti* (BMNH P 5231) that has a large lateral extrascapular, and all of these genera have large quadrate-shaped operculars whose size and orientation suggest that the post-temporals were also large. We expect that these features will prove to be diagnostic of the family when more material is discovered.

Finally, we draw attention to the point that the components of the ring centra of *Megalichthys*,

Ectosteorhachis and *Cladarosymblema* are solidly fused, although they may be incomplete dorsally along part of the vertebral column. Andrews & Westoll (1970b: 427–429) considered that this type of structure represents the culmination of 'a trend of increasing consolidation of the axial skeleton within the Rhipidistia', and that it also occurs within other stocks such as the one leading to *Rhizodopsis*. It may yet be possible to distinguish between the centra of *Rhizodopsis* and megalichthyids using such features as the nature of the lateral grooves and the lack of a periosteal surface on *Rhizodopsis*. For this reason we prefer not to list the character of the centra as a possible diagnostic feature until further investigation is complete.

In preparing the above diagnosis of the family some previously used features have had to be ignored in the light of new observations, and others have been stressed now that we have access to information derived from better preserved specimens. In particular, we note that Bjerring (1972), followed by Jarvik (1985), indicated that within the Osteolepiformes, the crista parotica of osteolepidids differs from that of rhizodontids in that it runs posteromedially beneath the skull roof, leaving the lateral parts of the supratemporal and the entire extratemporal unsupported by endocranium. To arrive at this conclusion they used the endocranium of *Ectosteorhachis nitidus* on which they superimposed the roof of *Megalichthys laticeps* as interpreted by Bjerring (1972). Their view has been confirmed, at least for osteolepids, by the genus *Gogonasus andrewsae* Long, new specimens of which are under description by us; but in our specimens of *C. narriense* the crista parotica runs posteriorly along the outer edge of the supratemporal, and our observation of *E. nitidus* indicates that it is precisely similar. Hence we do not accept that the position of this structure is consistent in all osteolepiforms, and it cannot have the significance they proposed. However, the position of the transverse wall of the endocranium at the rear of the trigeminofacialis chamber is probably a feature that will permit the differentiation of the Osteolepididae from the Megalichthyidae. The sharp lateral turn of this part of the endocranium where it attaches to the roofing bones, does seem to be a distinctive feature of the Megalichthyidae, even though the angle may be somewhat less than a right angle in *E. nitidus*. Romer (1937) figured this structure as oblique rather than transverse in its orientation, but we consider he was in error; the chamber has been partly excavated in

MCZ6499 without reaching the wall, which must therefore be more nearly transverse than he considered it to be.

Borgen (MS) pointed out that the first use of a family-level designation involving the use of the stem name *Megalichthys* was in a list published in 1902 by Hay. However, Hay did not define the family, and he included a number of genera that today would be regarded as only distantly related to *Megalichthys*. In 1962, Vorob'jeva considered that *Megalichthys*, as she then conceived it, was a Carboniferous form derived from an *Osteolepis* stock in the Middle Devonian, and she retained *Megalichthys* in the Osteolepididae. The discovery of Late Devonian megalichthyids in Turkey (Janvier, 1983) showed that the Devonian origin of the group is correct, although it may not extend back to the Middle Devonian. Vorob'jeva (1977) considered the Megalichthyinae to be one of a number of subfamilies, although she did not assign genera to it.

Young et al. (1992) defined the Megalichthyidae so as to include *Megalichthys*, *Ectosteorhachis*, *Megistolepis* and their new genus *Mahalalepis*. They used eight characters to diagnose the family. Seven were roofing characters of the ethmoid shield and the eighth was the presence of tusks on the premaxilla. Apart from the notching of the parietal to receive the posterior nasal, which is a very variable character (Thomson, 1964a: fig. 6), we accept this list but, with the exception of Long, we consider that it is too incomplete to meet the needs of an effective classification.

In this family we include *Megalichthys* Agassiz, *Ectosteorhachis* Cope, *Cladarosymblema* gen. nov., the new genus being described from Norway (Borgen, MS), and a form referred to as Megalichthyidae gen. et sp. nov. by Janvier (1983). The diagnostic characters cannot be observed on all these genera, but they are almost certainly present on *Megalichthys*, *Cladarosymblema* and Borgen's new genus. Most of the characters are known on the other two listed, and the apparent absence on the others is the result of a lack of data rather than the presence of different structures. Janvier's Turkish specimens consisted of an ethmoid unit and part of a mandible only, and consequently it is impossible to be certain of the assignment. However, it does have the characteristic flat snout, the tusk and pit on the premaxilla, the semblance of a divided prenasal fossa, a slit-like anterior naris, and olfactory canals separating at a low angle from a point behind the mid-length of the ethmoid unit. There

is a high probability that it is correctly assigned to the Megalichthyidae, although we remain uncertain about its generic relationships.

Megistolepis and *Mahalalepis*, which were placed by Young et al. (1992) in the family are, in our opinion, too poorly known to assign to the Megalichthyidae with confidence. *Megistolepis* is known from two Late Devonian species from Russia, neither of which shows adequate diagnostic features. However, we note that there is no tusk on the premaxilla and that, although the vomers are transverse in outline, they have two tusks or pits on each. The prenasal fossa is divided, and the figure given by Vorob'jeva (1977: fig. 35B) seems to show that the olfactory canals extend back to the posterior third of the ethmoid unit; both of these characters are known at present exclusively in members of the Megalichthyidae. Our view is that until more material is found, there are sufficient differences from the standard *Megalichthys* to make it unwise to assign this genus to a higher taxon. Vorob'jeva (1977) assigned it to the subfamily Megistolepinae of the family Osteolepididae.

Mahalalepis is known from a single fragmentary ethmoidal shield. Most of the characters we consider to be diagnostic of the family have not been preserved and so three of the authors of this paper are not prepared to comment further on its assignment. Long, however, still considers that on balance it is probably a megalichthyid.

Schultze (1988) placed *Lohsania* (Thomson & Vaughn, 1968) with *Ectosteorhachis* in the Megalichthyinae. Thomson & Vaughn made comparisons of the otico-occipital roof and the scales of *Lohsania* with *Ectosteorhachis*, but they pointed out that the structure of the vertebral centra differs in the two genera (Thomson & Vaughn, 1968: cf. figs 2 & 8). *Lohsania* lacks the structure of the centra found in *Ectosteorhachis*, *Megalichthys* or *Cladarosymblema*. In addition, the mandible of *Lohsania* is short and deep compared with that of *Ectosteorhachis*, but information on its other features remains unknown; no ethmoid or otico-occipital units were recovered from the same locality as the holotype, and hence the homogeneity of the paratype sample cannot be guaranteed. Although Schultze (1988) compared the new form he was describing from the Pennsylvanian of Kansas with *Lohsania*, the evidence of a relationship is restricted to a similarity in external outline, and even that is not great. We consider the mandible figured by Schultze (1988) cannot be definitely assigned. Until new data become available no worthwhile judgments can

be made about the taxonomic relationship of *Lohsania*.

Cladarosymblema gen. nov.

TYPE SPECIES

C. narrienense sp. nov. from the Raymond Formation, Early Carboniferous (Viséan), in the Drummond Basin, Queensland.

DIAGNOSIS

Lateral line canal in front of posterior nasal sharply deflected mesially. Lateral extrascapulars and post-temporals large. Denticulated anterior part of parasphenoid long, very acute, but terminating well behind median processes of vomers. Wide parasymphysial plate turned posteriorly at lateral extremities, and covered with small denticles; lateral ridge on coronoids reduced and devoid of denticles; postglenoid process large and well-rounded; prearticular produced into acute anterior termination, usually non-denticulate; lateral line pores large; no oral branch of lateral line canal in surangular.

ETYMOLOGY

Kladaros (Gr) = weak; sym (Gr) = together; blema (Gr) (n) = cover. Referring to the fact that the dermal bones and scales of the specimens have fallen apart during preservation.

REMARKS

The above diagnosis is a minimal statement distinguishing this new genus from other members of the family Megalichthyidae. We now discuss in detail the means by which the genus can be distinguished in turn from *Megalichthys*, *Ectosteorhachis* and the new Norwegian genus described by Borgen (MS), and we comment on other features likely to become useful with the advent of new knowledge.

Because material from the type locality of this new genus has been referred to previously as *Megalichthys*, or as being akin to *Megalichthys*, for example by Long (1989) and Turner (1993), it is important to be explicit about the differences between the two genera. Comparison between *Cladarosymblema* and *Megalichthys*, as represented by the type species *M. hibberti*, leaves no doubt that the two are distinct, although many differences are only in the relative proportions of various elements. We have examined some of the specimens in the Royal Scottish Museum, two in the Hancock Museum in Newcastle-upon-Tyne,



FIG. 5. *Cladarosymblema narrienense*. Dorsal view of the holotype, QMF21082. Scale: 10mm.

and a cast of the specimen from the Hunterian Museum, Glasgow, on which Jarvik's (1966) description was based. In addition we have used an advance copy of Borgen's review of the European species of *Megalichthys* (Borgen, MS).

One obvious difference is the size of the pores in the snout, those of *Megalichthys* being very large, and those of *Cladarosymblema* much smaller. We have considered the possibility that this difference is related to size of the specimens examined, or to resorption of tissue from the rims of the pores during cosmine replacement, but it seems more likely to be a taxonomic feature. A second obvious difference is the more anterior position of the external narial opening in *Cladarosymblema*, a feature it shares with *Ectosteorhachis* and Borgen's new genus from Norway. The posterior process on the prearticular that carries the tusk is shorter in *Cladarosymblema* than in *Megalichthys*, the tusks are more anteriorly placed, and the teeth on the margin of the premaxilla anterior to the tusks are more reduced or even absent. The number and position of the postrostrals is also a possible means of differentiating *Megalichthys* from *Cladarosymblema*, but in both genera the number of specimens in which the bone boundaries are not obscured by cosmine is small, and among the useful ones the variation is too large for definite conclusions to be reached. (We have already noted our reservations about the taxonomic use of these bones.)

More information is needed on the endocranium of *M. hibberti* to make an adequate comparison of the endocranium of *Cladarosymblema*; the main description available is that of Jarvik (1966), which deals with the ethmoid unit only. We disagree with Jarvik about some important parts of the anatomy of this unit. In particular, we consider it possible that the posterior process of the vomer is not as he claimed; it seems more likely that the bone he interpreted as this process is a cracked piece of the surface of the endocranium. We do not accept that there is an intervomerine pit in the position he indicated. There are other foramina on the endocranium lateral to the posterior end of the parasphenoid, in addition to those indicated by Jarvik. These will be commented upon in the appropriate places below. We now comment on differences between *Megalichthys* and *Cladarosymblema* in dermal characters.

Examination of well-preserved specimens of *M. hibberti* has convinced us that no inter-premaxillary bone (Schultze, 1974) is present, and that the tusk and pit seen in this region are on the premaxilla. Several specimens of *C. narrienense* in which the radiation centres and boundaries of the bones can be discerned on internal and external surfaces (Fig. 27A,D), show no evidence of

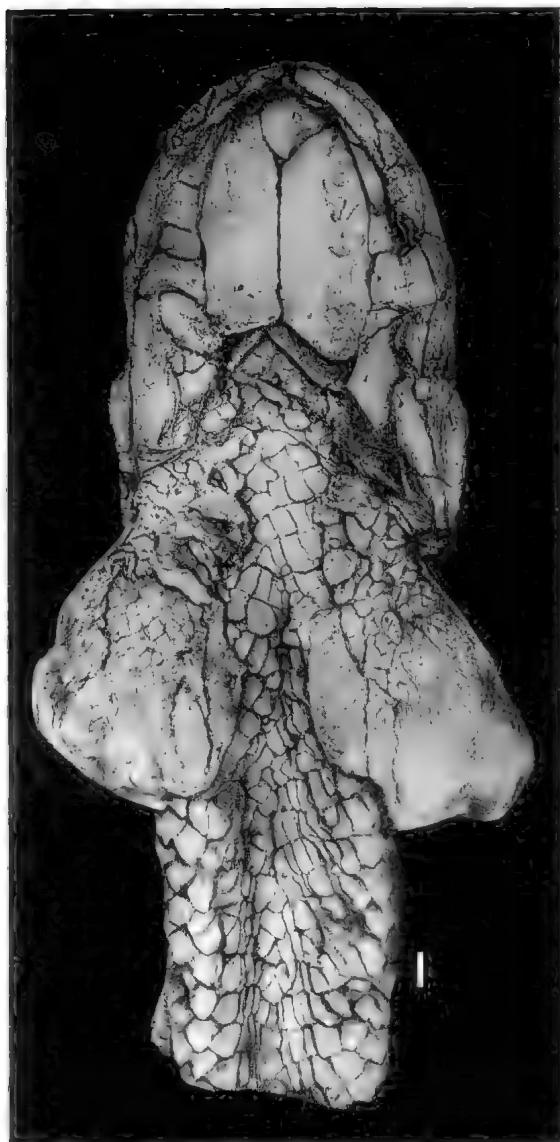


FIG. 6. *Cladrosymblema narrienense*. Ventral view of a cast of the holotype, QMF21082, made prior to the removal of the left gular and submandibular plates and the scales on the ventral surface of the lobe of the left pectoral fin. Scale: 10mm.

an inter-premaxilla either, and hence we do not consider this point further.

C. narrienense and some specimens of *M. hibberti* have similarly shaped parietals, which are deeply notched anterolaterally to receive the posterior nasal and are widest immediately behind the nasal. Thomson (1964a: fig. 6) illustrated several variants of this basic shape in *M. hibberti*, but the usual form is very similar to that in *C.*

narrienense. Hence we do not consider this to be a useful feature for distinguishing the two genera.

The skull roof of the otico-occipital unit of *Megalichthys* is best known from *M. laticeps* (Bjerring, 1972) and the work on *M. hibberti* by Borgen (MS). The relationship between *M. laticeps* and *M. hibberti* is not well understood, and indeed the two may be conspecific. Bjerring (1972) described a remarkable branch of the supraorbital lateral line canal extending into the postparietal, and Borgen (MS) has illustrated a specimen of *M. hibberti* in which remnants of the canals are visible on the visceral surface of the postparietal. X-rays, and the broken surfaces of bones, show that no such canal is present in *C. narrienense*. The transverse pit-line on *C. narrienense* is continuous across the postparietal and tabular bones, and turns backwards slightly at its lateral extremity. A shorter posterior line runs posterolaterally from near the inner end of the main line, but the two do not join. In *M. hibberti* the transverse line is variable (Borgen, MS); in some specimens it is continuous across the postparietal and tabular bones, but in others it is a short discrete segment on each bone. Bjerring also inferred from the shape of the tabular (his supratemporal) that a small extratemporal must have been present, although it had not been observed by previous workers. All of our specimens of *C. narrienense* in which this part is preserved, show an edge on the supratemporal for the articulation of an extratemporal, and on some specimens a small branch of the lateral line canal extends into the space that would have been occupied by such a bone. We conclude that an extratemporal was present, but its shape remains conjectural.

The endocranium of the otico-occipital unit of *M. hibberti* is so poorly known that comparisons with *C. narrienense* are not possible.

According to Schultze (1974), the olfactory tracts of *Megalichthys* sp., cf. *M. hibberti* from the U.S.A. diverge from the braincase at c.90°, the division lying about one-third of the length of the ethmoid unit from its anterior end. Jarvik (1985) considered that the evidence for this was dubious, and certainly it is true that the preservation of the specimen figured by Schultze leaves something to be desired. However, *C. narrienense*, preserved in the same way, shows that Schultze's interpretation of that specimen is probably correct. Despite this we consider that it is necessary to confirm that the British specimens of *M. hibberti* share this arrangement. The limited available evidence implies that they do not do so.

In comparison with *Cladarosymblema*, *Ectosteorhachis* has less club-shaped postparietals, a weaker notch in the parietals for the posterior nasals, strongly tuberculate cosmine (Thomson, 1975), wider and less acute anterior denticulate part of the parasphenoid (Thomson, 1964a,b), an otico-occipital unit making a strong processus connectens (Romer, 1937), a more oblique orientation of the endocranium forming the posterior wall of the trigeminofacialis chamber (Romer, 1937). (Our direct examination of Romer's material, shows that his reconstruction is inaccurate in respect to the last point, and the wall in question is more nearly transverse than he showed.)

The mandibles of the two genera provide several useful distinguishing features. The adductor fossa is longer and broader in *Ectosteorhachis*, the coronoids have a row of denticles along their lateral edges, and these are continuous with the denticles on the parasymphysial plate; *Cladarosymblema* has no denticles on the lateral edges of the coronoids. In *Ectosteorhachis* the denticles on the prearticular are more robust and extend to the anterior end of that bone, whereas in *Cladarosymblema* they are much weaker and, if they reach the anterior end, they are limited to the dorsal edge. One of Romer's specimens, MCZ6999, has an unknown number of small, approximately equidimensional submandibulars that are certainly more numerous than the 6-7 in *Cladarosymblema*. On the other hand, Thomson (1975: fig. 36) has illustrated a specimen with submandibulars not unlike those of *Cladarosymblema*, although still numbering 8-9. We are unable to judge the significance of these data.

Cladarosymblema narrienense sp. nov.

MATERIAL EXAMINED

HOLOTYPE: QMF21082, the anterior part of a fish including the skull, pectoral fins, and part of the scale-covered trunk (Figs 5-6); collected from the fine-grained sandstone immediately above the limestone about 1 km north of the Police Mountain Track (Fig. 2). **PARATYPES:** QMF21083-21111; 26537-26576; 31858-31907; 33046-33058: Same locality as the holotype.

DIAGNOSIS

As for genus.

ETYMOLOGY

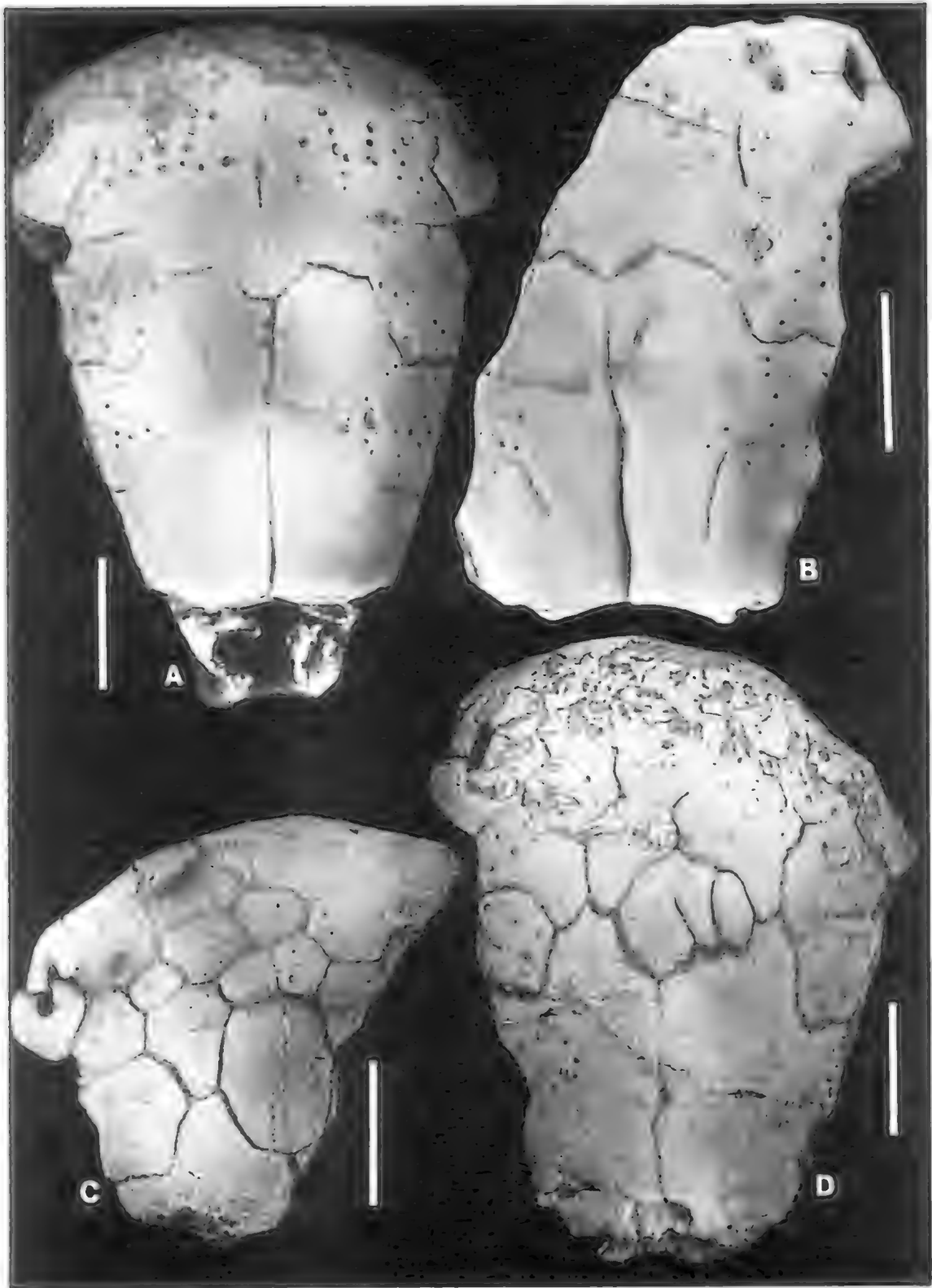
From the Narrien Range, the dominant topographical feature in the vicinity of the outcrop at the type locality.

DESCRIPTION

EXTERNAL DERMAL BONES OF THE SKULL

Ethmoid Unit. Two relatively complete roofs of the ethmoid unit (QMF21083 and 21110), seven other large fragments, several smaller fragments including an isolated premaxilla, and several detached rostral ends are known. The ethmoid unit withstands erosion better than the more posterior parts of the skull because it has a downturned rim and a marginal thickening of the premaxilla. The dermal bones of the unit are completely covered with cosmine; an occasional plate shows a weak blister, but none shows the blistered texture that accompanied regrowth in *Ectosteorhachis*. On the anterior half of the roof cosmine has obliterated sutures making identification of individual bones difficult. However, QMF21097 (Figs 7C,E; 8C), 21095 (Fig. 7F-I) and 21111 (Fig. 27C-D) show these bone outlines almost completely, the first on the external surface and the others on the internal surface.

On QMF21083, 21108 and 21110 the parietals are well preserved (Figs 7A,B,D; 8A,B,D); on the holotype, weathering has removed detail from central parts of the parietals, and lateral outlines are indistinct. Parietals occupy slightly more than half the length of the ethmoid unit. The interparietal suture is almost straight, but with a slight irregularity over its posterior half in some individuals. There is no pineal foramen. The parietal outline is distinctive with an anteromesial projection and a deep anterolateral angle to accommodate the most posterior nasal. The widest part of the parietal is at the suture with the posterior nasal, behind which is a gradual taper to the posterior margin of the shield. In some specimens this taper is straight-edged and in others it has a slight double embayment. We assume that a supraorbital and an intertemporal articulated with the parietal, although no examples of these bones have been found. The supraorbital part of the lateral line canal passes from a posterolateral direction into the parietal, slightly anterior to the midlength of the intertemporal notch, and exits through the anterolateral edge of the parietal. A strong arcuate anterior pit-line lies on the posterior third of the bone but fails to reach the median suture.



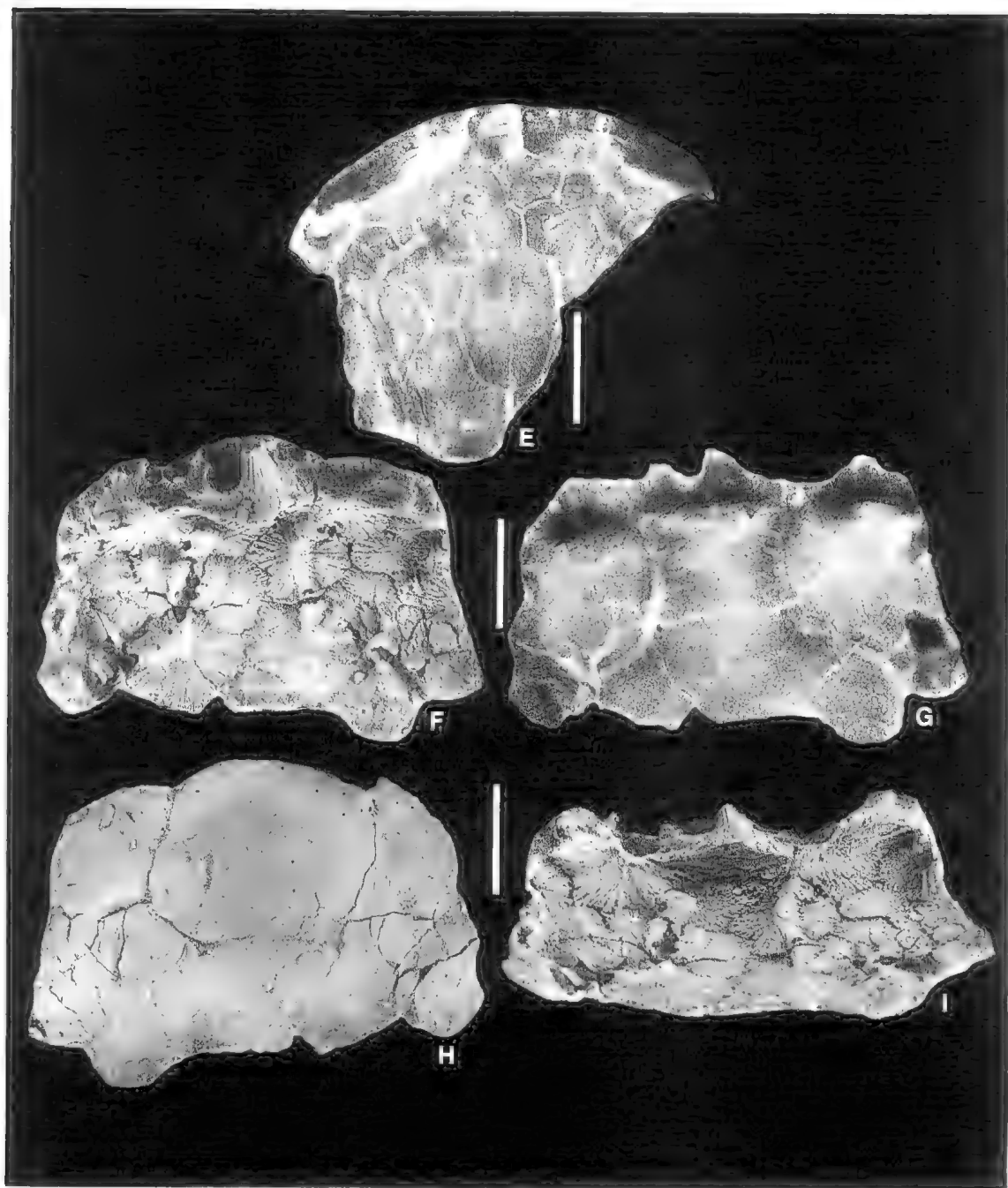


FIG. 7. *Cladarosymblema narrienense*. A-I, views of the roofs of isolated incomplete ethmoid units showing variation of dermal bone patterns. In A and B, QMF21083 & 21108, the more rostral sutures have been obliterated by cosmine. C, QMF21097 shows the most extensive suture pattern found. D, QMF21110 has incomplete sutures rostrally, but shows extensive resorption of cosmine in patches and growth of a number of cosmine blisters. E, X-radiograph of QMF21097 figured in C. F, G, QMF21095 in ventral view and X-radiograph in same orientation, showing radiation centres of dermal bones and the course of the lateral line canals. H, I, dorsal and posteroventral views of the same specimen. Note radiation centres and lateral line canals in F and I, and cutaneous sensory pore clusters on all dorsal views except D. Scales: 10mm.

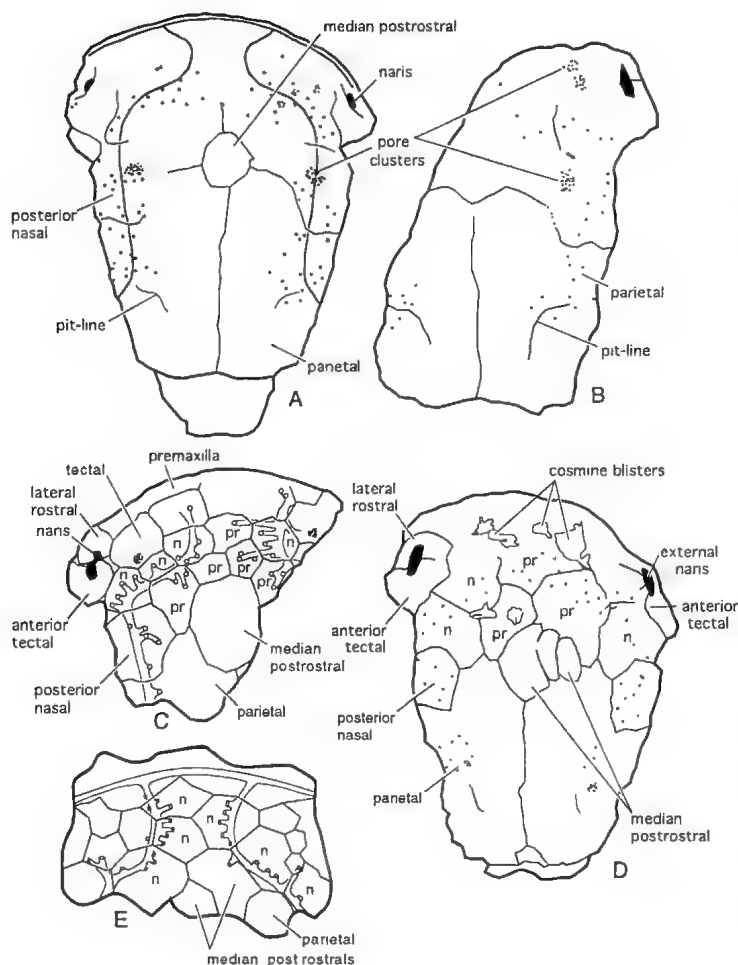


FIG. 8. Outline diagrams of specimens shown in Fig. 7. Lateral line canals are drawn from X-radiographs, and the bone outlines reconstructed from all sources. A, QMF21083. B, QMF21108. C, QMF21097. D, QMF21110. E, QMF21095. n = nasals; pr = postrostrals.

QMF21083, 21097, 21111 and 21547 each have a single symmetrically placed median postrostral, but QMF21110 (Figs 7D; 8D) has three asymmetrical bones occupying the same space; in QMF21108 overgrowth by cosmine has almost obliterated the sutures between the median postrostral and surrounding bones (Figs 7B; 8B). Between the premaxilla, the median postrostral and the anterior tectals and lateral rostrals, the roof is covered by small irregular bones (Figs 7C,D,E; 8C,D,E; 27A,C,D). Identification of the bones of the nasal and postrostral series is a problem. Nasals are normally recognised by the presence of the lateral line canal, and the postrostrals lie between the canals

anterior to the median postrostral. QMF21095, 21097, 21111 and 26540 are very instructive in this context, because the endocranial material has been stripped away revealing the pores opening to the external surface, the centres of radiation of the dermal bones and, deeply buried in the dermal bones, the lateral line canals whose position and size can be checked by X-radiography. These canals do not pass through the centres of ossification of most of the bones (Figs 7E,F,G; 8C,E). Instead, they often bypass the bone centres or run along the sutures. For example, the left side of Fig. 7E and 8C shows the canal lying along the suture between the most posterior postrostral and the neighboring small nasal, and Fig. 7F-G show the canals partly along sutures on both sides of the specimen. The variable distribution of lateral line pores reflects great variation in the length of the tubules from the main canals. For example, the right side of Fig. 7E shows extremely long tubules from the supraorbital canal extending mesially into bones we label as postrostrals, and Fig. 27D also shows long mesially directed tubules. This variation makes it impossible to use the pores to locate the canals precisely. Be-

cause the canals cannot be unambiguously positioned from a study of the pores on the external surface, and in places the canal is not unequivocally in one bone or its neighbour, the recognition of nasals and postrostrals is frequently ambiguous.

In Figs 7F,G, 8C,E and 27D, the canal swings sharply anteromesially on emerging from the posterior nasal, but its course relative to the bones of this region varies from specimen to specimen. On the left in Figs 7F,G and 8E it passes through the anterolateral corner of the bone flanking the median postrostral. Presumably, therefore, strict application of the definitions implies this bone has to be a nasal. On the right the bone that

unambiguously carries the canal is not in contact with what appears to be the median postrostral if only one of them is present. As shown in Fig. 7D and 8D, however, more than one may be present. We therefore consider that one interpretation of Fig. 8E is that it has two median postrostrals. Alternatively, the right one of the pair so labelled could be a postrostral like that on the left of the median postrostral in Fig. 8C. In the more anterior nasals, the canal turns forwards and slightly laterally to join the infraorbital canal in the premaxilla in the usual osteolepiform manner. The nasals from the two sides meet medially, and so in this specimen the only definite postrostral is the median. A similar absence of postrostrals has been inferred for QMF21111 (Fig. 27D), although the situation is not so clear. However, in QMF21097 (Fig. 7C, E), which has all the bones visible on the external surface, three small bones lie between the nasals and in front of the median postrostral; these can only be postrostrals. In addition, the bone anterolateral to the median postrostral on the left side has the canal along its suture, whereas the equivalently placed bone on the right clearly has the canal in its anterolateral corner. The bone on the left could be considered a postrostral and the one on the right a nasal. This seems to us to be entirely arbitrary, and we label them both as postrostrals. In this specimen, the nasals do not meet medially, and the intervening space is occupied by at least three small postrostrals. We conclude that the number of postrostrals is highly variable in this species.

Small tectals are present on all specimens, between the lateral line canal-bearing bones and the circumnaries, although these are usually not visible on the external surface due to the cosmine cover. They are best observed by X-ray or by cleaning the internal surface (Figs 7E-I; 8C,E; 27A,C,D). Their number and size varies between specimens and on opposite sides of a single specimen. On Fig. 7G a strong offshoot from the supraorbital canal enters the posteriormost of these bones on each side of the specimen. On the left side of Figs 7C and 8C,E, a small tectal bearing a sensory pit cluster lies on the mesial side of the lateral rostral, and on the right side a similarly placed bone is present, although no lateral rostral is preserved. Also, on the flank of the left premaxilla in Fig. 27A, tectals can be recognised from their radiation centres. We see no value at present in trying to homologise individual bones in the series.

The premaxilla is complete or near complete in three individuals in which the whole roof of the

ethmoid unit is preserved (the holotype, QMF21083, and 21110), as well as in five fragments (QMF21095, 21097, 21104, 21105, 21111) consisting of the bone itself and a few small more posterior bones adhering to its edge (Figs 7A,C,F-I; 8A,C,E; 21A,C; 22; 27A-D). In all of these specimens, cosmine has obscured the sutures between the premaxilla and its neighbours. The premaxilla is transverse and follows a broad arc across the front of the upper jaw. It has a strongly thickened bar across its inner surface, and this joins the endocranium; this rim produces a distinct furrow along its inner surface behind the teeth. On each side of the midline along the edge of the bone there are 16-20 small teeth, all of approximately the same size. Towards its lateral extremities the posterior face of this inner bar of premaxillary bone is marked by a posterior-facing area of horizontal grooves and ridges (Figs 21A; 22; 25D) that seem to have met the similarly ridged anterolateral surface of the vomers. At the median suture, some specimens (QMF21097, 21104) show a tusk on one side and a pit on the other (Fig. 20A), but in others two tusks are present side by side (Figs 21A; 22). To make room for these two tusks, the premaxilla is swept back into a short process that lies on the endocranial internasal ridge. This median process is relatively much shorter than its equivalent in *Megalichthys hibberti*, and does not extend back almost to the parasphenoid as Jarvik (1966: figs 17,19) indicated for that species. In some of our specimens, the row of small marginal teeth does not extend across the front of the tusks, but on QMF21083, 21095 and 26541, small teeth do occur in this position, and on QMF26540 a row of even smaller teeth crosses in front of at least the left tusk, the edge of the right bone being missing. These differences are probably individual variants.

The deeply buried infraorbital canal, which runs in the thickened bar across the inner face of the premaxilla, is joined by the supraorbital canal at the ossification centre of the bone. The infraorbital canal opens laterally either in the apex of the lachrymal notch or along the limb of the premaxilla that borders the notch ventrally, but never in the lateral rostral. Consequently, the maxilla, which does not carry the lateral line, must have met the premaxilla only below the opening for the canal; most, if not all, of the notch would therefore have been occupied by the end of the lachrymal. We can find no evidence of a premaxillary canal in the position shown by Jarvik (1966: fig. 14C) for *Megalichthys hibberti*.

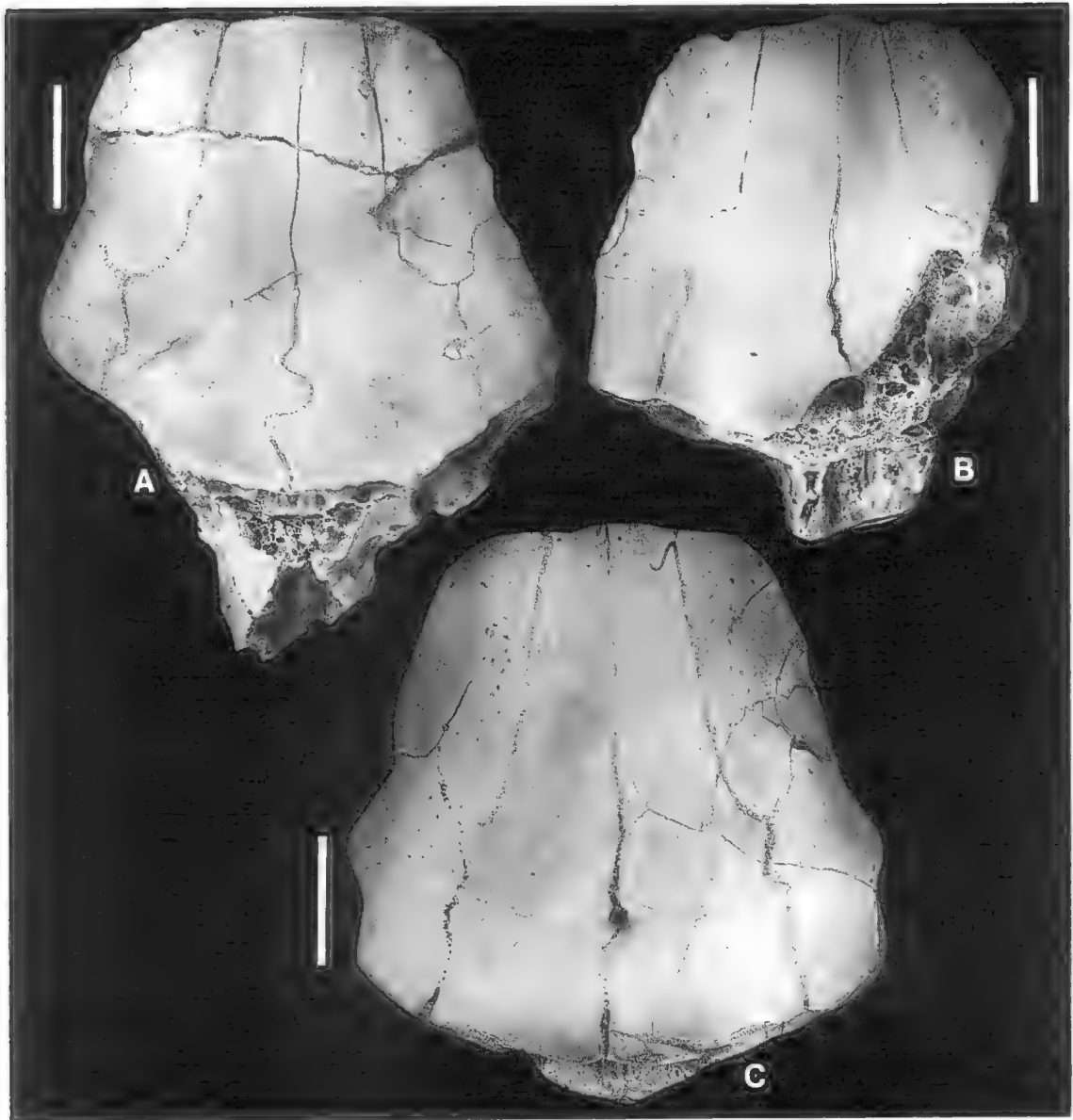


FIG. 9. *Cladarosymblema narrienense*. Dorsal views of the roofs of three otico-occipital units. A, QMF21085 with highly flexed median suture. Compare with holotype. B, QMF21084 has well-developed cutaneous sensory pore patches on the supratemporals. C, QMF21096 has two peculiar features: the apparent foramen in the mid-line, and sutures in the anterior end of the postparietal and the posterior end of the supratemporal. All of these are indicated on Fig. 10. Scale: 10 mm.

In that figure he shows the infraorbital canal in the lateral rostral, and a more ventrally placed canal in the premaxilla. We consider that one of these canals, probably the one in the premaxilla, is the true infraorbital, and the other one is an offshoot from it. The lateral line in the premaxilla opens to the external surface *via* an irregular row of pores just above the edge of the lip. Internally,

it opens behind the teeth in a row of pores; these may be large (Fig. 20A), a mixture of large and small (Fig. 21A,C), or small throughout (Fig. 27A,C). Even the largest pores have edges of finished bone, so their size is not a consequence of the etching process. Pores in this position would scarcely have carried seismosensory neuromasts, nor are they effectively placed to house

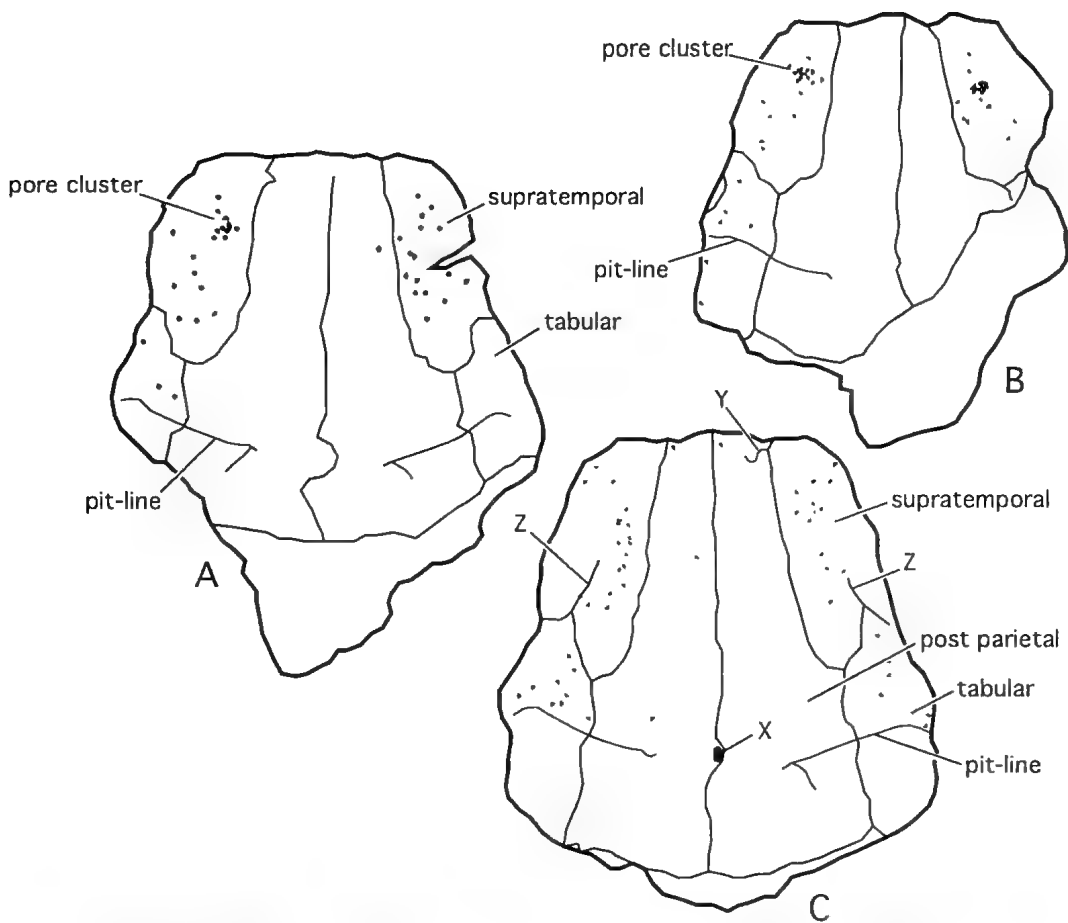


FIG. 10. Outline drawings of the same specimens as Fig. 9. X is an anomalous foramen, and Y and Z are anomalous sutures.

electrosensory receptors. On the other hand, they would be well situated to serve a chemosensory function. We conclude that the lateral line canal in this region carried a variety of nerve fibres.

There is no groove between the premaxilla and the adjacent parts of the circumnarial bones as Westoll (1937, 1940) claimed for *Eusthenopteron* and other osteolepidids (but cf. Panchen, 1967: 394). The lateral line canal in *Cladarosymblema* passes more ventrally, from the premaxilla to the lachrymal; it does not enter the circumnarial bones. This may be considered to raise a question about our identification of the lateral rostral, which is usually thought to carry the infraorbital canal in its anterolateral projection (Jarvik, 1966: fig. 14). We are of the opinion that the presence of the canal in the lateral rostral has not been established in all megalichthyids, and await fur-

ther data on this matter before considering the issue seriously.

QMF21111 shows a second sensory system in the snout. Internally, subjacent to the premaxilla, the median postrostral and intervening bones, an array of ossified tubules passes through the vesicular endocranial bone (Fig. 27C). These tubules are clearly not of dermal origin, and follow a different course from the lateral line canals in the overlying bones, as can be seen by superimposing Figs 27C and D. A branch of the main tubule trunk runs across the front of the median postrostral and turns back in the midline to meet its antimerere. The main trunk runs anteromesially beneath the nasals and postrostrals and subdivides to form a ramifying series of tubules. Along the edge of the endocranium, where it is sutured against the palatal lamina of the premaxilla, these tubules open into foramina and then into the front

wall of the nasal capsules. They also communicate in some places *via* short cross-tubules with the lateral line canals. In QMF21110, an ethmoid fragment that has had the palatal region eroded away exposing the mid-levels of the endocranium (Fig. 21C), the tubules do not occur more deeply in the vesicular endocranial bone. Although we have no specimen that offers unequivocal information, the tubules probably connect posteriorly with foramina in the antorbital wall, interpreted as carrying branches of the profundus superficialis V or ophthalmicus superficialis VII or both. The restriction of the tubules to the region immediately underlying the dermal bones suggests that they were not part of a blood vascular system supplying tissues in the snout generally.

These tubules are not approximately straight, do not bifurcate in the same way, and are fewer in number than the ramifying tubules in the snouts of Devonian dipnoans (Campbell & Barwick, 1982, 1984, 1987; Cheng, 1989), in *Diabolepis* (Chang & Smith, 1992) and in *Youngolepis* (Chang, 1982, 1991). We are not convinced that the tubules in the two groups are homologous. (See Functional Interpretations: Tubules in the Snout, for further discussion.)

Groups or patches of pores that lie in slight depressions have been observed on all ethmoid units, although their distribution is not symmetrical on all individuals and they do not occur on all specimens in the same places. Jarvik (1966: fig. 15) referred to these as 'special cutaneous sensory organs'. The patches contain any number of pores from 4 to 45. The individual pores are generally separate, but on some individuals two or more are enclosed within a rim that is usually bent and may even be U-shaped (Fig. 7A-C). The most common dispositions of the pore patches are as follows: one on each posterior nasal; one just above the lip in the angle between the supraorbital and the commissural canals; one or two mesial to the external narial opening; and one posteromesial to the external narial opening. Each patch is close to a lateral line canal if not actually in a lateral line bone, but we have not been able to establish a connection between the pores and the lateral lines. On the contrary, QMF21111 shows pores on the inner surface of a bone that has a patch of pores externally, suggesting that they open directly to the internal surface. Other patches show no evidence of such openings internally, nor any connection with the lateral line canals.

Because of cosmine cover, only QMF21097 and 21110 show evidence of a suture between the lateral rostral and the anterior tectal dorsal to the

narial opening, although these bones are clearly sutured ventral to the opening on several specimens. The two bones are normally distinguishable on the internal surface, and are approximately the same size. The pattern of circumnarial bones is more similar to that of *Ectosteorhachis nitudus* (Thomson, 1964a) than *Megalichthys hibberti* (Borgen, MS).

Surprisingly well-preserved circumnarial bones bear fine denticles arising from the surfaces lining the narial opening (Fig. 28B,C). These are usually isolated and bear a single pointed cusp, but some are bi-cuspid or even tri-cuspid (e.g., QMF21108, 21110, 21111). Denticles occur on all specimens in which this region is well preserved, so there is no doubt about their reality. They occur on both dorsal and ventral surfaces of the circumnarial bones, and although they vary in extent between different individuals, no part of the rim seems consistently free of them, and on QMF21108 they are densely distributed around the entire rim (Fig. 28C). Apparently such structures have not previously been described in other osteolepiforms. Borgen (MS) has noted abraded tubercles (or minute foramina) in a similar position in his new megalichthyid from Norway. It seems likely that the denticles are so small that they could not be exposed in their entirety by the mechanical preparation of his specimens. Distribution of these denticles puts constraints on the reconstruction of soft tissue structures such as glands, hypothesised for *Eusthenopteron* and *Megalichthys* (Jarvik, 1966, 1980). It is highly improbable that glandular tissue would have been situated on the surfaces described.

When viewed through the ventral opening of the nasal capsule of better preserved specimens, much of the dorsolateral wall of the capsule is made of lateral rostral and anterior tectal bones, their inner surfaces crossed by more or less concentric striations (Fig. 28A-C). The nature of these striations is not obvious, but it is probable that the cartilage of the wall of the nasal capsule was applied to this surface. The surfaces and edges of these bones are finished, showing no signs of breakage, and the endocranium laps on to their sides making a clear sutural contact. We have carefully examined the edges of these bones in view of the importance that has been attached to the existence of the 'processus dermintermedius' and the 'processus tectalis' by Jarvik. In some individuals, (QMF21108 and possibly QMF21111), much of the internal rim projects inwards beyond the adjacent parts of the capsule lateral wall. However, this projection

constitutes the rim itself and seems never to form a thin flange that arises from the rim as in *Eusthenopteron foordi* (Jarvik, 1942, 1966, 1980) and *Gogonasus* (Long 1985a, 1988). The projecting part of the rim in *Cladarosymblema* has both lateral rostral and anterior tectal components; that is, it includes parts of the rim that could give rise to 'dermintermedius' and 'tectalis' processes. QMF21083, our best preserved specimen, shows that the rim does not project far enough to occlude any part of the fenestra endochoanalis beneath, as Rosen et al. (1981:191) claimed for *Eusthenopteron*; nor does the processus dermintermedius or tectalis occlude any part of the fenestra endochoanalis in the holotype of *Gogonasus* (ANU21885). No endocranial tissue, such as in Jarvik's (1966) 'processus intermedius', takes part in the formation of the ventral rim or flange; nor is there a 'processus palatinus' or passage for an infraorbital sensory canal, as in *Megalichthys* (Jarvik, 1966:73). Jarvik (1966) illustrated a depression in the posterior part of the 'dermintermedius' and thought that this may have housed a lateral nasal gland (see caption for his fig. 12). Our specimens show no discrete depression in that position, although QMF21083 has a slight embayment in the outline of the flange in the appropriate position (Fig. 28B,C). In that specimen, the embayment is in the tectal rather than the 'dermintermedius', and we consider it to be without anatomical significance. As already noted, the distribution of denticles across all of these surfaces precludes their association with glands in any case. In sum, we see no evidence that the nasal capsule in *Cladarosymblema* was subdivided in the way Jarvik has reported in *Eusthenopteron* and *Megalichthys*.

Otico-occipital Unit. We have five well-preserved (QMF21056, 21084, 21085, 21086 and 21094) and several fragmentary examples of the roof of this unit. Our specimens retain only the postparietals, the supratemporals and the tabulars (Figs 9-10).

The postparietals are the largest bones in the entire roof, and in our view their posterior edge forms the anatomical limit of the skull roof (Romer, 1941). From their anterior extremities, the postparietals widen gradually to the level of the posterior edge of the supratemporals where they abruptly expand; thereafter they continue to expand gradually to the rear of the shield. Consequently, the bone has a distinctive outline. The postparietals extend more posteriorly than the tabulars and have only a very faint notch at the median suture. This median suture is straight

anteriorly, but is mildly to strongly zigzag on the posterior third in different individuals (compare Fig. 9A,C). The supratemporals are widest just behind their midlength, having a small facet anteriorly for the intertemporal and a thickened edge for the articulation of the postorbital extending almost the entire length of the bone. At the posterolateral corner of the supratemporal there is always a notch for the spiracular fenestra, which seems to have extended back onto the flanks of the tabular (Figs 9; 29). A distinct facet on the posterolateral edge of the tabular was for the articulation of the extratemporal. That bone is not preserved on any of our specimens. In its overall pattern, the otico-occipital shield closely resembles that of *Megalichthys laticeps*, as described by Bjerring (1972).

For the articulation of the ethmoid unit, the anterior edge of the supratemporal has a device that is similar to that in *Megalichthys laticeps* (Bjerring, 1972). A flat supratemporal process (fronto-dermosphenotic of Bjerring) on the supratemporal extends forwards beneath the intertemporal; this process has a deeply grooved ventral surface (Fig. 29A,B). Dorsal to the process is a transverse socket that articulated with the reciprocal edge of the intertemporal. On its inner edge, this socket is continuous with a deep posteriorly directed groove that runs along the side of the braincase.

Well-preserved posterior edges of skull tables (Figs 9A,C; 38A,B) show that the tabular and the outer part of the postparietal have a slit in the edge of the bone, the lip below the slit extending posteriorly to form a shelf for the articulation of the lateral extrascapulars. Mesially the situation is quite different. Under the mesial part of the postparietals, the endocranium is tightly appressed to the dermal bone and extends posteriorly beyond its edge to make a platform for the articulation of the median extrascapular; no slit occurs in the edge of the dermal bone.

The course of the lateral line canals has been observed by tracing the pores on the surface, by the position of openings on broken bone surfaces, and by X-radiographs (Fig. 30). The canal enters the skull table at the posterolateral corner of the tabular and runs forward through the length of the supratemporal to emerge just lateral to the supratemporal process. A branch, which seems to be represented by more than one ramus, runs from the tabular into the postulated extratemporal. Unlike *Megalichthys laticeps*, *Cladarosymblema* has no branch of the lateral line canal from the

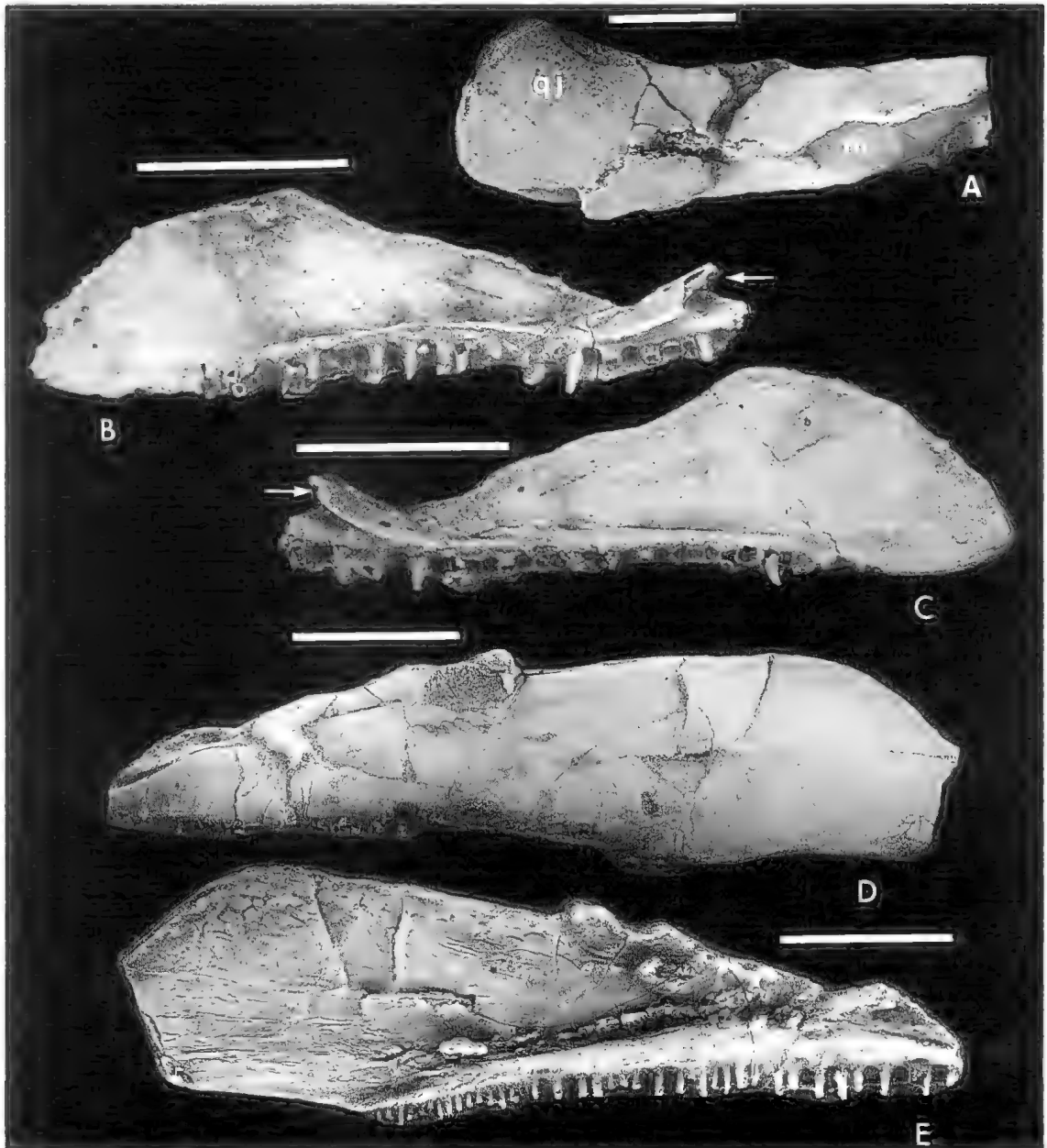


FIG. 11. A, lateral view of right quadratojugal (qj) and the posterior part of maxilla (m) of the holotype of *Cladarosymblema narrienense*, QMF21082. B,C, internal views of left and right maxillae of *Gogonasus andrewsae*, ANU49259, showing ridge dorsal to the tooth bases and extending forwards into a flange (arrow) that forms the posterior edge of the choana. D,E, external and internal views of an almost complete left maxilla of *Cladarosymblema narrienense*, QMF26551. Note the posterior edge is not quite complete, the true shape of this part of the bone shown on Figs 11A and 14B. The anterior end is also slightly incomplete, but the posterior edge of the choana is partly represented. Scale: 10mm.

supratemporal into the postparietal, and the postparietals have no pores on their surfaces.

Pit-lines are not deeply inscribed, but they can be distinguished on five specimens (QMF21056,

21084, 21085, 21086 and 21098). The longer one runs from the postparietal anterolaterally across the tabular and is slightly deflected posteriorly, before terminating just inside its lateral margin

(Fig. 10A,C). A shorter branch, restricted to the postparietal, runs posterolaterally from the inner end of this line.

A reconstruction of the whole roof of the species is given in Fig. 14A.

Maxilla and Cheek. No complete cheek is available, but its main features can be reconstructed from the maxilla, quadratojugal, squamosal, jugal and postorbital. The posterior position of the maximum height of the maxilla, the large quadratojugal, the almost equidimensional outline of the squamosal, the relationship of the lachrymal to the maxilla, and the shape of the anterior edge of the opercular, enable us to say that the cheek was relatively shorter than in other osteolepiforms, and that the vertical axis of the preopercular was almost at right angles to the line forming the ventral edge of the maxilla (Fig. 14B).

Three maxillae are known, two broken ones in position on the holotype, and a third without its posterior tip that was isolated by acid etching (Fig. 11D,E). Its height/length ratio is 0.28. Its highest point is towards the rear, adjacent to the quadratojugal. At its anterior end, QMF26551 has a peculiar disruption of the cosmine, giving the appearance of being a composite structure. However, we can see no evidence of two centres of ossification in the X-radiographs. Anteriorly, adjacent to the disrupted cosmine, is a patch of special cutaneous sensory pores similar to those on the skull roof. Jarvik (1966: fig. 15A) showed a similarly placed patch in *Megalichthys*. Unlike that of *Megalichthys*, however, the maxilla of *Cladarosymblema* shows no openings to the infraorbital sensory canal, which was confined to a more dorsal position within the lachrymal.

There has been endless argument about the existence of a choana in osteolepiforms. Rosen et al. (1981) claimed that what had been interpreted as a choana in *Eusthenopteron*, the best known osteolepiform genus, was in fact a pit for the reception of a mandibular tusk. This statement has caused much confusion; the summary of the matter given by Chang Mee-mann (1991) still expressed reservations about the reliability of the

data. In the light of this, the material described herein offers vital support for the existence of a choana in osteolepiforms. On the dorsal side of the anterior tip of the maxilla is a triangular process that articulates, in part, with the lachrymal, while anteriorly the maxilla abutted the premaxilla. In *Gogonasmus* this process has an overfolded tip which, when the maxilla is reassembled against the palatine bones and the premaxilla, forms the posterior margin to an ovate opening that is ideally placed to be the choana. The process on the specimen of *Cladarosymblema* is worn and does not show this feature in detail, but what is preserved indicates that it was of the *Gogonasmus* type. It is important for the understanding of the osteolepiforms in general to note that the *Gogonasmus* structure is also present on the isolated maxilla (Fig. 12C) from the de Bretzel specimen, which is described in the ADDENDUM to this paper. Thus it seems clear that a choana is present in primitive osteolepiforms and, as Long (1988) recognised, there is no evidence that the cavity in the palate of *Gogonasmus* is for the reception of a tusk from the upper jaw. Confusion about the presence of a choana in osteolepiforms is now dispelled.

More posteriorly on the maxilla two protuberances, both of which carry cosmine, break the dorsal outline. The overlapped edge behind these protuberances is short and narrow for articulation with the lachrymal, whereas the posterodorsal edge behind the maximum height is finished and bevelled, and is gently convex in outline. The posterior extremity of this specimen is broken off, but its outline can be inferred from the shape of the anteroventral edge of the quadratojugal against which it would have fitted. This shows that the maxilla was produced to a posteroventral point, which is unlike the bone in any other osteolepiform genus with which we are familiar apart from *Megalichthys hiberni* (Borgen, MS). The internal surface of the maxilla is generally smooth, but close to its ventral edge it has a thickened ridge, highest anteriorly and gradually decreasing in thickness and height to the posterior end of the tooth row. This ridge is quite different

overleaf on p.124

FIG. 12. *Cladarosymblema* sp. Illustrations of specimens isolated from a limestone block collected from the roadside, and are described in the ADDENDUM. A,B, external and internal views of an isolated right lachrymal, QMF26522E, showing the posterior overlap and the dorsal articulatory process and groove. C, internal view of isolated right maxilla, QMF26522A, with posterior end and extreme anterior tip broken off. Note the flange (arrow) bordering the choana as in *Gogonasmus*, Fig.11B. D, isolated left lateral extrascapular, QMF26522H; anterior to the left. E, roof of an incomplete ethmoidal unit, QMF26522. Print electronically retouched. Note the large median postrostral and the pore cluster on the posterior nasal. Scale: 10 mm.

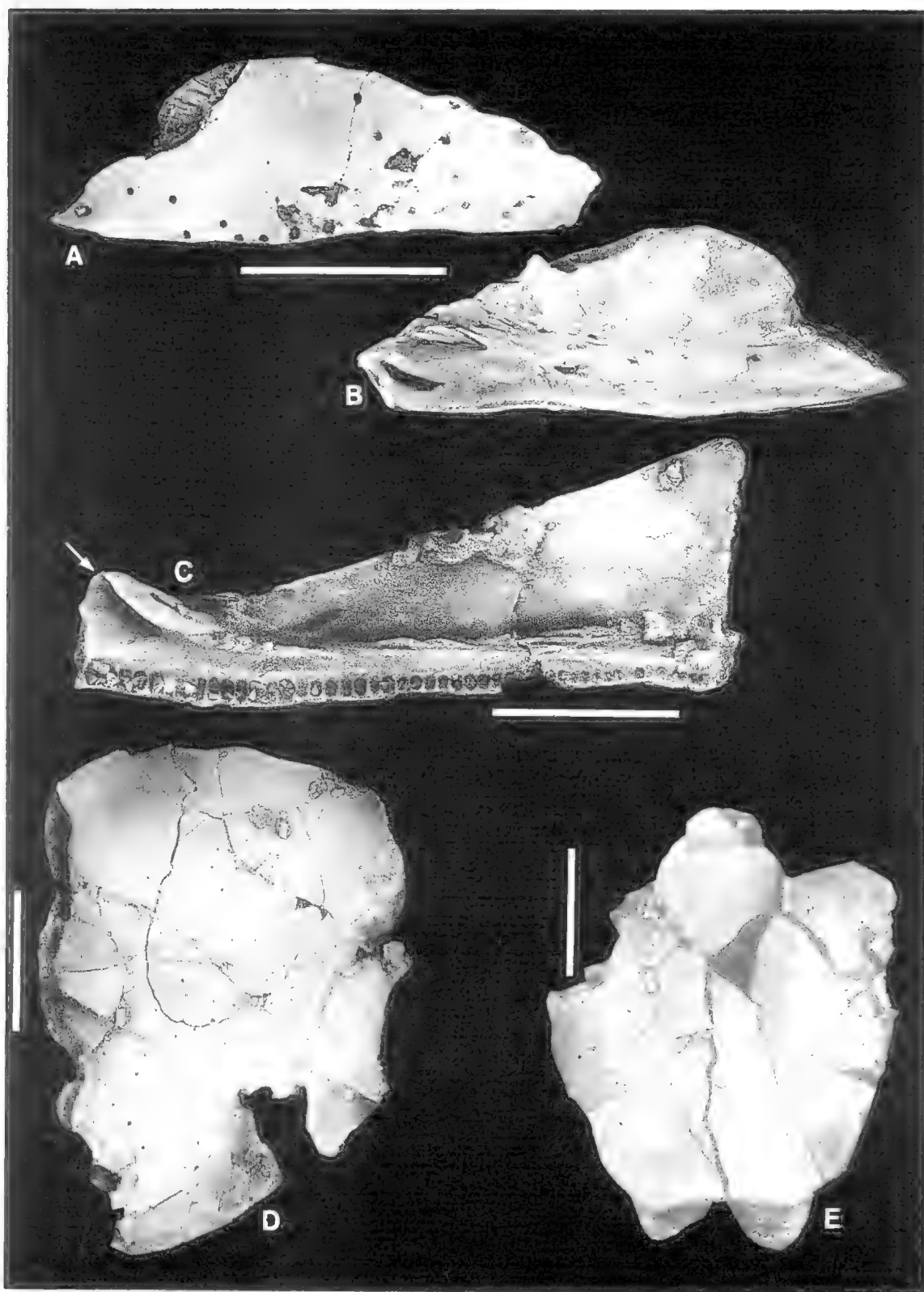


FIG. 12.

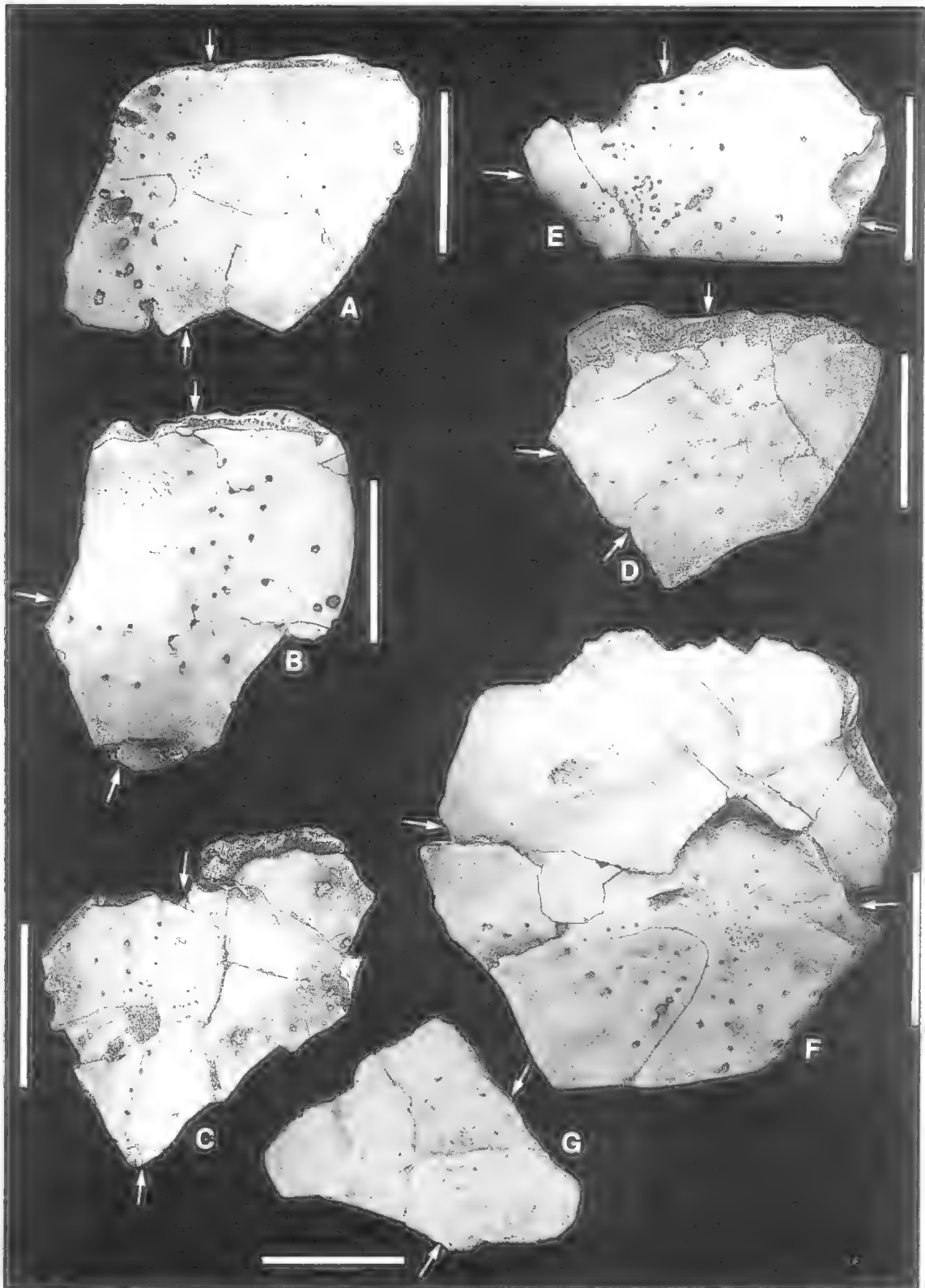


FIG. 13.

in shape from the one in *Megalichthys hibberti* (Borgen, MS).

The quadratojugal is present on both sides of the holotype. Its height is c.0.6 of its length, and its shape is distinctive, having a strong dorsal embayment with an overlapped edge for the squamosal, and a sigmoid outline anteriorly for the maxilla; these intersect to produce an acute angle at its anterodorsal edge (Fig. 11A). The posterior edge of the bone is broadly convex. A vertical pit-line is present at its anterior third. We have been unable to distinguish lateral line pores on its surface; these would be expected if the bone carried the preopercular canal. We conclude that the preopercular bone carrying its canal passed posterior to the quadratojugal. This interpretation is in accord with the posterior outline of the quadratojugal, which swings forwards dorsally in an unusual way for an osteolepiform, to make a pronounced posterodorsal angle.

A fractured almost complete right squamosal (Fig. 13F) with its posterior and dorsal edges broken was identified by the slight overlap on its anterior and anteroventral edges; the lateral line passing along its length; and the long highly arcuate pit-line, which is flexed posteriorly at its dorsal end and joins with the quadratojugal pit-line at its ventral end. Its outline has been reconstructed from X-radiographs and the preserved edges. Contact with the maxilla is short to vanishingly small. Along the edge with the post-orbital is a marked underlap, and a much narrower one along the edge with the jugal. Pores from the lateral line occur over the lower half of the surface. The pit-line is formed as a single row of pits spaced 7 per mm. Two patches of small sensory pores occur anteroventrally, opening among the pores of the lateral line.

An almost complete jugal (Fig. 13E) is longer than high, and has a finished ventral edge where it overlapped the maxilla. The dorsal edge changes character along its length; anterodorsally there is a bevelled orbital margin, behind which there is a short prominent overlapped flange; posterior to this, the edge is grooved for the reception of the postorbital. The anterior edge of

the jugal is largely overlapped by the lachrymal, whereas its posterior edge is incomplete. The lateral line canals are strong, the jugal branch being close to the ventral margin as it enters from the lachrymal, and it diverges from the ventral edge posteriorly. The canal is slightly flexed where it joins the infraorbital canal. A large patch of sensory pores lies near the junction of the two canals and a smaller patch just dorsal to it.

One isolated almost complete plate, QMF33057, is interpreted as a postorbital because it carries an undivided lateral line canal, has an overlapped edge against what would be the jugal, and an edge which could be an orbital margin. The evidence is not conclusive. The bone is illustrated in Fig. 13G. As will be apparent from the reconstruction given in Fig. 14, it is difficult to fit the plate precisely into the space left between the surrounding bones, but we assume that individual variation accounts for the main part of the problem. The preserved bone is sub-triangular in shape. The points of emergence of the canal are clear, and a small patch of cutaneous sensory pits occurs over the canal in a similar position to the patch in *Osteolepis* (Jarvik, 1948: fig. 36A).

By matching the pit-line on the quadratojugal of the holotype with that on the isolated squamosal, it is possible to orient these two bones convincingly. Their posterior edges then stand almost normal to the ventral edge of the quadratojugal. Knowing these features and the shape of the anterior edge of the opercular, we estimate that the preopercular was a high, short, vertically-oriented bone, with a gently convex posterior edge. A reconstruction of the cheek of *Cladarosymblema* is given in Fig. 14B.

The cheeks of *M. hibberti* and *E. nitidus* are poorly known. Thomson (1964a: fig. 2A,B) produced schematic reconstructions of the cheeks of both species, but without supporting evidence. We have no means of assessing their validity, and hence have to ignore them in assessing similarities with *Cladarosymblema*. Borgen (MS) presented drawings of a specimen of *M. hibberti* that is too crushed to permit a reconstruction, but it is clear that the jugal is short and the quadratojugal

previous page

FIG. 13. *Cladarosymblema narrienense*. A,C, left post-temporals, QMF31873 and 26537. A small piece has been broken out of the posterior edge to the right of the lateral line in A; otherwise its margins are entire. Note the pit-line and the pore cluster on each figure. B,D, lateral extrascapulars, QMF31871 and 31876. B has most of the anterior margin and a small part of the extreme posterior margin preserved. C has a complete anterior margin, but all other margins are broken. E, isolated right jugal, QMF31874. The orbital margin is on the upper right. F, isolated right squamosal, QMF 26575. G, an isolated left postorbital, QMF33057. In all figures, arrows indicate emergent points of lateral lines. Scale: 10mm.

high; he also produced information on the shape of the maxilla of *M. hibberti* and his new genus from Norway. We conclude that the high posterior point of the maxilla, the relatively short squamosal and the high quadratojugal, make a community of characters that differentiate this group of species from members of the Osteolepididae. Hence we consider that the cheek shape is probably of familial significance.

Gulars and Submandibulars.

These are known from the holotype and several isolated gulars, QMF26543, 26544, 26549, 26561, 26562 and 31880 (Figs 6; 16B-D). The principal gular on the holotype is a large bone the width of which is c.40% of its length. The entire lateral edge shows overlap for articulation with the submandibulars, but the posterior third shows deeper embayments for the more posterior submandibulars and the subopercular 2 (Figs 6; 16B). Isolated plates show an anteromedial embayment for the overlapping median gular, and overlapped areas laterally for the submandibulars, the width of the overlap increasing posteriorly in Fig. 16D and on the unillustrated QMF26549. The overlap is broken off posteriorly in Fig. 16C. The left principal gular slightly overlaps the right, at least anteriorly. The only posteromedial edge preserved intact suggests that if there were any overlap it was very small. It seems most likely that the two principal gulars lay almost edge to edge. The surface is cosmine-covered, but the anterior half shows variable resorption patterns. The holotype shows a small patch of resorption rings on its anterior half (Fig. 16B), but QMF31880 has a remarkable pattern (Fig. 16D). This consists of a series of narrow, irregular, resorption channels that isolate patches of cosmine with highly irregular sizes and shapes, a pattern that is nothing like the standard Westoll-line resorption pattern found in most dipnoans. At the

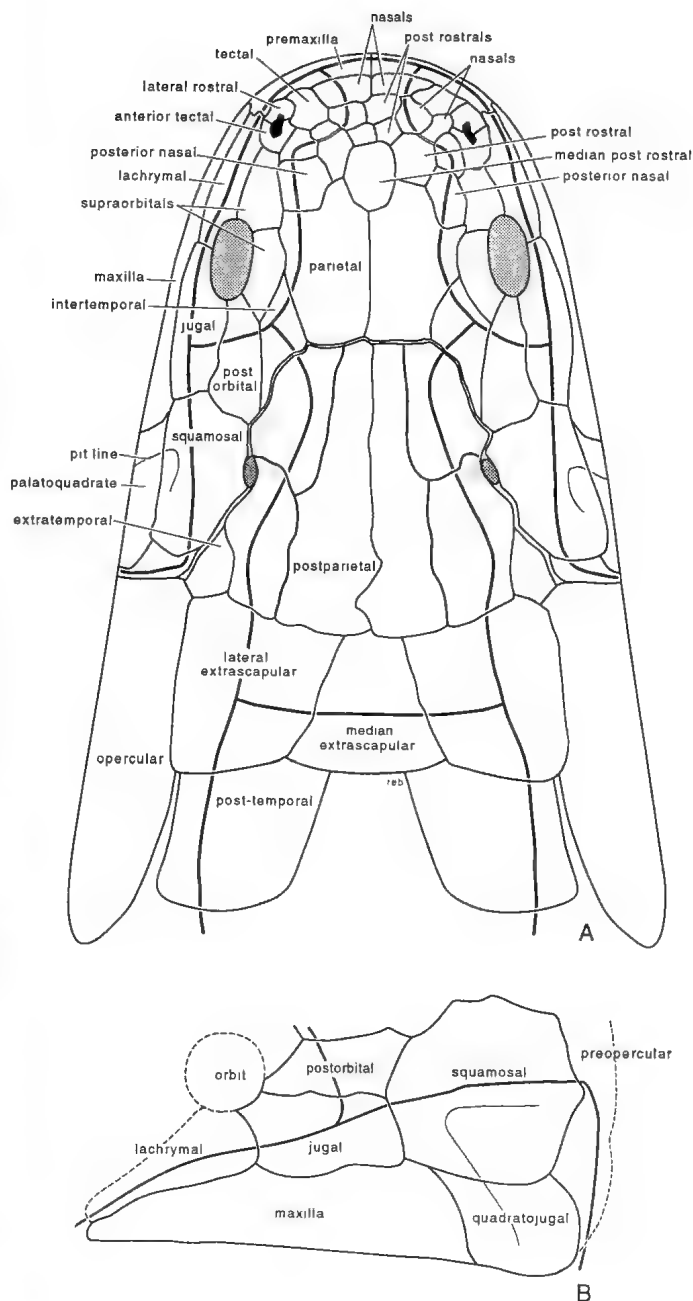


FIG. 14. *Cladarosymblema narrienense*. A, Reconstruction of skull roof based on all available data. B, Reconstruction of the cheek using the holotype for the relationship of the maxilla to the quadratojugal, and isolated jugal and squamosal plates. The lachrymal and the preopercular are based on the positions of the adjacent bones, and hence have dotted outlines.

centre of these resorption rings is a patch of newly formed cosmine with entire margins, and on the outer side of the rings is an irregular edge formed by resorption that was actively resorbing at the time of death. This is exactly like the pattern observed on some scales, and in our view represents the standard mode of cosmine replacement for the genus.

The median gular (Figs 6; 16B) is large compared with that of *Megalichthys hibberti*, but approximately the same relative size as that of the new genus from Norway (Borgen, MS). It is c.30% the length of the principal gulars. We cannot discern a pit line on it. Its anterolateral edges are embayed to receive the anterior submandibulars, producing a median point. Posterolaterally, it overlaps the principal gular on each side.

The number of submandibulars is six on one side, and six or possibly seven on the other (Figs 6; 16B). The most anterior one is very long and thin, and extends around the anterior end of the median gular to meet its antimere. We see no evidence of a median bone in the series. Instead the median gular has an anterolateral embayment on each side to take the first submandibular, thus giving its anterior edge a pointed outline. The second submandibular is of similar proportions to the first, but the more posterior plates are progressively shorter. On the right, the most posterior plate is much wider than long; on the left, length and width are approximately equal. As noted above, the submandibulars of *E. nitidus* are smaller and more numerous than those of *C. narrienense*. A specimen of *M. hibberti* numbered G8.50 in the Hancock Museum, Newcastle-upon-Tyne, figured by Birks (1916: pl. 13) and examined by us, shows a similar number of submandibulars to *C. narrienense*, although the lateral ones are not as elongated as in that species.

Operculars. Both operculars are present on the holotype, but they are broken. Six other isolated specimens, QMF21092, 21093, 21103, 26538, 26545 and 26550, are better preserved (Fig. 15D,E). The operculars are large bones, about 60% the length of the two skull units together, and their height is only a little less than their length. The anterior and anterodorsal edges are almost straight, and the posterior is broadly convex. The anterior edge shows a distinct projection anterodorsally, interpreted as an articulation; the remainder of this edge is bevelled and slightly roughened where it was overlapped by the preopercular. The anterior half of the dorsal edge has a lenticular overlapped surface for the lateral

extrascapular, but posterior to that the edge is finished and curves around to the posterior margin. This implies that as the post-temporal has no overlapped lateral edge, these two bones must have abutted edge-to-edge or were separated by a slight gap.

Running across the surface posteroventrally from the articulatory process is a broadly rounded ridge, marking a flexure in the bone that gradually diminishes in prominence posteriorly. This presumably reflects the cross-section of the body of the animal. In anterior profile, dorsal to this ridge the opercular is inflected at c.55° to the main surface of the bone. Apart from the anterior and anterodorsal edges, the entire external surface is cosmine-covered.

Towards the anterodorsal corner of all observed operculars, the external surface shows a patch of special cutaneous sensory pores of the kind seen elsewhere on the skull. These are in the same position as the pores on the opercular of *M. hibberti* figured by Moy-Thomas (1935: fig. 2). The number of pores in a patch varies from 19 to c.80. No connection between these pore patches and any underlying structure has been established. Obviously, no lateral line canal occurs in the opercular, but on the inner surface of QMF21105 is a groove that does not extend to the edge of the bone. This could be regarded as evidence of the presence of a nerve beneath the appropriate part of the opercular to innervate the pore group, but the fact that it is seen on only one of the available specimens suggests that it is probably only an individual variant of no significance.

The internal surfaces of the operculars are not well preserved, but anterodorsally in the depression formed by the bone flexure, QMF21093 shows two slight scars which were probably for the attachment of ligaments from the hyomandibular. QMF21103 has a slight scar in the same region, but this has been emphasized by weathering and its significance is in doubt.

Subopercular 1, which is only 85% of the length of the opercular in the holotype, is overlapped dorsally by the opercular. In addition, an incomplete individual, QMF26553 (Fig. 15F,G), is confidently identified as a first subopercular. Cosmine covers its entire external surface except for the dorsal and anterior edges, which have a deep band of rough tissue indicating overlap by adjacent bones. The dorsal overlap is highest anteriorly where it has a distinct dorsal projection, and it decreases in height gradually posteriorly. Its anterior edge has a protrusion in line with

the flexure mentioned below, and the anterior overlapped area becomes smaller ventrally, disappearing completely at the ventral edge of the bone. The bone has a pronounced, subangular longitudinal flexure about 5–6 mm below the dorsal cosmine margin. In the anterodorsal corner of the bone is another group of special sensory pores like those on the opercular.

Subopercular 2 is smaller, being 66% of the length of the first in the holotype; it too is cosmine-covered. One almost complete isolated subopercular 2, QMF33056, has been recovered; only its posterodorsal margin is missing (Fig. 15H,I). The bone tapers posteriorly. The dorsal edge has a deeply overlapped surface for subopercular 1, but its extent cannot be determined. Anteriorly a narrower edge was overlapped by the posterior submandibular and the principal gular; the bone is thickest where this edge joins the cosmine-covered part. A large group of sensory pores lies in the cosmine towards its anterodorsal edge. This group contains a high proportion of two or more pores that lie surrounded by ridges containing flask chambers (Fig. 15I), but it has not been possible to remove the sediment to observe the number of pores forming these subgroups. On the inner surface of the bone beneath the pore-covered patch, a number of openings occur, but without destroying the specimen it is not possible to determine if they open through to the outer surface. Judging from its similarity to the second subopercular of *Gogonasmus*, a single isolated fragment, QMF26552, represents the anterior third of this bone. The two suboperculars meet behind the last submandibular (Figs 6; 16B), making a pattern like that of *Megalichthys hibberti*.

The reconstruction of *M. hibberti* by Miall (1885) shows only two suboperculars, but Moy-Thomas (1935) figured four bones in this position on the lectotype, which was chosen and figured by Agassiz, and refigured by Andrews (1982: fig. 8j). It seems to have only two suboperculars, but

the drawing leaves room for doubt. A well-preserved specimen, G8.80 from the Hancock Museum, was illustrated by Birks (1916), and his figure is consistent with Miall's interpretation. We have examined this specimen, and conclude that, at least in this respect, Birks was correct. It is clear that two suboperculars are present in this species as in *C. narrienense* and the new genus from Norway (Borgen, MS).

We note that other osteolepiforms, such as *Eusthenopteron foordi*, have only one bone that is normally identified as a subopercular, but also that there is a second plate lying at the posterior end of the submandibular series, called the submandibulo-branchiostegal plate by Jarvik (1944). This is undoubtedly homologous with our second subopercular. We prefer our terminology for this bone because the first subopercular extends down into the line of the submandibulars and the plate in question continues the line of the operculars. In addition, although the overlaps in *Cladrosymblema* are not completely clear, those in *Gogonasmus* are quite unambiguous (Figs 15A–C). In that genus, the second subopercular is clearly overlapped by the first subopercular, and its anterodorsal corner has a projection like the other subopercular. In other words, its relationships are such that it lies in the opercular series and is morphologically like an opercular rather than a submandibular.

Extrascapulars and Post-temporals. The lateral extrascapular is well represented by two isolated specimens, QMF31871 and 31876 (Fig. 13B,D). It is subtriangular in outline, but with all edges slightly curved. The anterior margin bears a narrow overlapped surface; its lateral edge, the shape of which is also known from the overlapped dorsal edge of the opercular, is finished. Its mesial edge is not well enough preserved to describe. The specimens are readily recognised by the junction of the main lateral line and the occipital commissure.

overleaf on p.130

FIG. 15. Opercular and subopercular bones of *Gogonasmus andrewsae* Long, and *C. narrienense*. A–C, opercular, and suboperculars 1 and 2 from the left side of *G. andrewsae*, ANU49259. Note distinctive overlaps as described in the text. D–E, two isolated right operculars of *C. narrienense*, QMF21092 and 21103. Note cutaneous sensory pore clusters (arrows) towards the anterodorsal corners, small on D, much larger on E, and the large erosion hole in the centre of D. F–G, two isolated fragments of the left subopercular 1 of *C. narrienense*, QMF26553 and 26550. Note similarity in shape to the subopercular 1 of *G. andrewsae* illustrated in B, and cutaneous sensory pore clusters (arrows) of different sizes in the anterodorsal corners. H, an almost complete subopercular 2, QMF33056, missing only its posterodorsal edge. Arrow shows cutaneous sensory pore cluster. I, enlargement of ventral part of sensory pore cluster from the anterodorsal corner of the same specimen. Scale: 10 mm; except I: 1 mm.

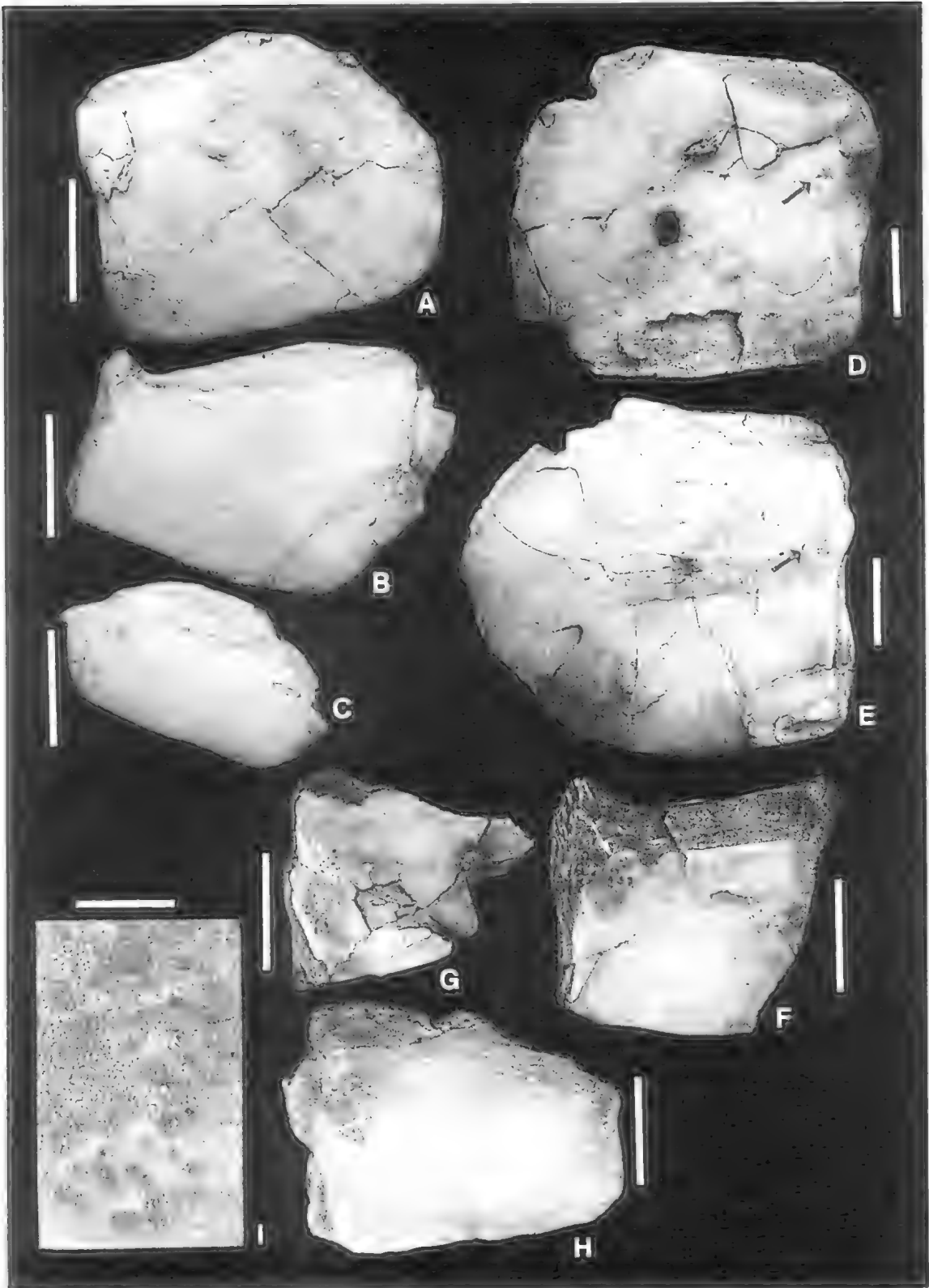


FIG. 15

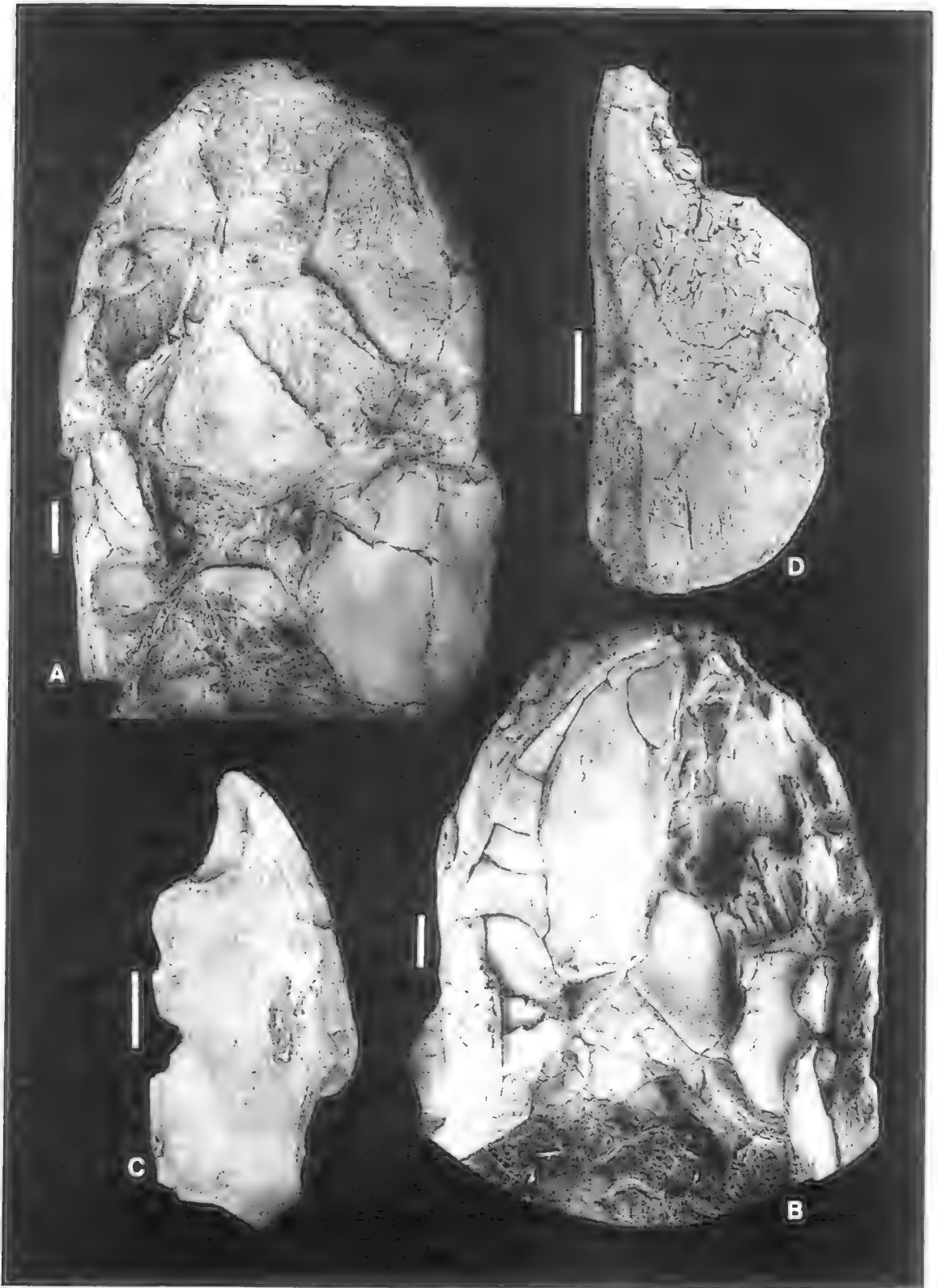


FIG. 16

On the holotype an incomplete fragment of bone lies between the operculars on the dorsal surface. This fragment could represent the only median extrascapular in the collection. Space requirements and the shape of the lateral extrascapulars show that the median extrascapular must have been narrow anteriorly and rapidly expanded posteriorly, its lateral margins bearing overlapped surfaces. Two left post-temporals, QMF31873 and 26537, are known (Fig. 13A,C). The former specimen is the more complete. It is cosmine-covered, sub-rhombic in outline, but the anterior edge is slightly wider than the posterior. The anterior edge bears a slight overlap which is divided into two parts, representing contact with the median and lateral extrascapulars. All other edges are finished, and bevelled on the inner surface, indicating that they overlapped adjacent bones. The lateral line is in the left half of the bone, and seems to run a straight course. A mainly transverse hook-shaped pit-line is present on the lateral half also, and a patch of sensory pores lies mesial to the bend in the hook. This bone is large in comparison with those of *Eusthenopteron* and other osteolepidids, and its anterior overlap is small. The fact that it is almost completely covered with cosmine is also unusual, but we note the presence of patches of cosmine on both the anocleithrum and the supracleithrum. Although it cannot be demonstrated from the material available, a process of the supracleithrum probably extended between the opercular and the post-temporal (Fig. 14A).

PALATAL BONES.

The bones of the palate of *Cladarosymblema* are not well known.

Vomers. The vomers are represented by four isolated incomplete specimens, each of which has a large tusk and associated pit, and a high wall around the anterior edge that carries up to 20 denticles along its crest (Figs 18;19). The anterior crest apparently diminished in height abruptly mesial to the more mesially placed tusk, or its replacement pit. The denticles along the crest are not all of the one size, nor are they confined to a single row. As all the specimens in Fig. 18 show, the largest denticles are restricted to the anteromesial side of the mesial tusk or its replacement pit. Smaller denticles lie in a row in front of

these larger ones, but this row is not continued laterally in front of the lateral tusk on two of the three available specimens. On the third, QMF26558 (Fig. 18D,E), the row is also continued around the lateral tusk.

The front wall of the vomer is high and almost vertical. Its surface is smooth except for a patch of horizontal ridges (Fig. 18F) that would have articulated with the similar ridges on the premaxilla.

The holotype has the crushed left vomer exposed by excavation. It seems to have the median process almost complete, but it is so fractured that interpretation of its features is difficult. No median process is preserved on any of the isolated specimens, but the broken end of the process is shown on Fig. 18G,H. The extent of this median process can be judged from the attachment areas for the vomers on the endocranium (Fig. 20A; 21A); these are very transverse and have mesial extensions that meet or almost meet in the midline (see description of these surfaces below). We conclude that a depressed median process was present, but was broken off the isolated specimens. The vomers, therefore, are comparable with those of *M. hibberti*.

QMF26556, in which the lateral side of the vomer is almost complete, shows a notch that may mark the passage of the maxillary branch of cranial nerve V to the nasal capsule, as Thomson (1964b:328) has hypothesised for *Ectosteorhachis* and Jarvik (1942: fig. 61) for *Eusthenopteron*.

Pterygoid. Despite continued attempts, no pterygoids or other palatal bones have been recovered by etching. Excavation of the holotype has exposed part of the endopterygoid, but nothing significant can be said about it.

Parasphenoid *. The parasphenoid is a bone of dermal origin, closely applied as a thin sheet over much of the base of the endocranium. However, owing to deficiencies of preservation, the complete limits of the parasphenoid are impossible to determine in any one specimen of *Cladarosymblema*. However, by careful examination of several specimens on which parts of the parasphenoid are preserved (Fig. 20A,B,D), a reasonably accurate composite picture of the bone can be constructed.

previous page

FIG. 16. *Cladarosymblema narrienense*. A-B, dorsal and ventral views of the skull of the holotype, QMF21082. In B, the left side of the gular and submandibular series has been removed to expose the palate, the clavicle, subopercular 2 and the broken subopercular 1. C-D, right and left principal gular plates, QMF26544 and 31880, showing general form, nature of the overlaps, and peculiar resorption and regrowth pattern of the cosmine. Scale: 10mm.

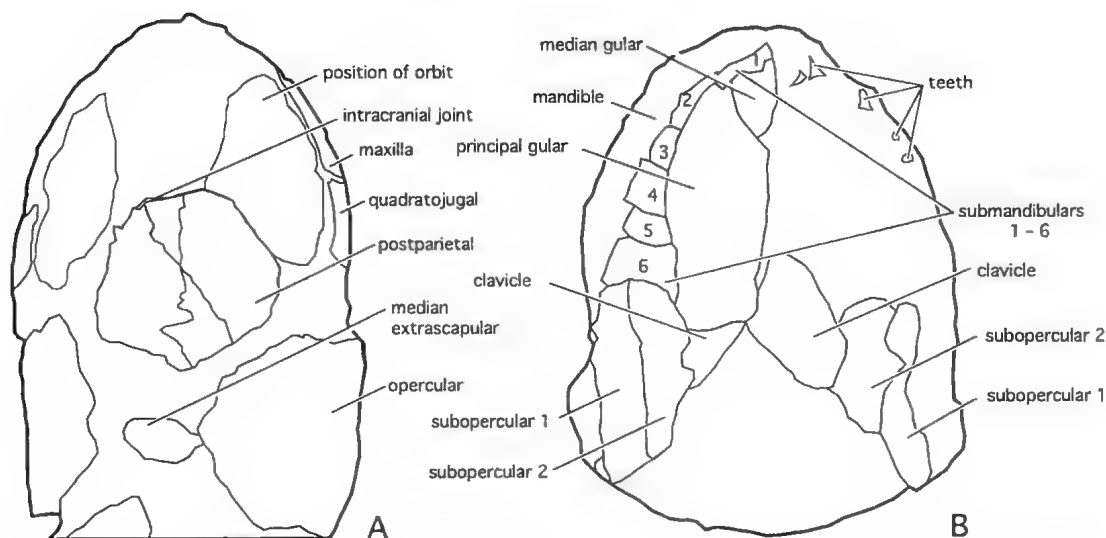


FIG. 17. *Cladarosymblema narrienense*. A-B, labelled outline drawings of views of the head of the holotype as shown in Fig. 16A-B.

The anterior limit of the parasphenoid is clearly shown on QMF21104, where it can be followed along an irregularly transverse line well behind the vomers (Figs 20A; 22); medially a smooth ridge, which is the extension of the denticulated surface, extends forwards of this transverse line. A broad, flat area of endocranial bone is exposed between the vomers and the parasphenoid, in contrast to the condition that Jarvik (1966) has shown in *Megalichthys* and that Thomson (1964a) has described in *Ectosteorhachis* (but see Romer, 1937:19). As noted above, the parasphenoid in *Cladarosymblema* does not border the prenasal fossae nor does it meet the posterior process of the premaxilla along the midline. Posteriorly from its anterior transverse limit, the parasphenoid sheathes the entire width of the palatal exposure of the endocranium between the pterygoquadrates and, as described by Romer (1937) in *Ectosteorhachis*, it sends an 'ascending process' well up the flanks of the basipterygoid process (see QMF21083); it does not, however, ascend the endocranial wall more anteriorly. Anterior to the basipterygoid process, the parasphenoid terminates at the edge of the subocular shelf.

The central part of the parasphenoid is dominated by a raised denticulated surface that, as in *Megalichthys* and *Ectosteorhachis*, is well rounded in posterior outline, but unlike in those genera it tapers to an acute anterior termination; it is bordered by a shelf-like expansion of the bone laterally. The depth of the denticulated sur-

face below the lateral expansion is greatest posteriorly and diminishes regularly towards the front. The central part of the denticulated surface is somewhat depressed (Fig. 20B,D) and has relatively few teeth (see QMF21105, 26547). Posteriorly the denticulated surface is bounded by a narrow rim of dense periosteal bone. The denticles, when completely preserved, are sharp cones, but in the specimens at hand, most are broken off or worn, leaving a basal annulus of enamel and dentine enclosing a central pulp canal. The buccohypophysial foramen, which is conspicuous in our specimens, is encircled by a ring of smaller denticles. Posterior to the denticulated surface, the parasphenoid forms a thin layer closely appressed to the endocranium as far back as the edge of the notochordal pit (Figs 20B,D; 21A; 22; 25D).

ETHMOIDAL ENDOCRANIUM

The endocranium of the ethmoid unit is known in some detail from five specimens, none of which is complete (Figs 20-27). Of these specimens, QMF21083 is the best preserved, QMF21104 has lost the dermal roof and part of the endocranium, QMF21110 has lost all of the endocranium except that immediately under the skull roof, QMF21108 has only the right side preserved, and QMF21105 retains only the ventral surface of the palate that is well preserved. Consequently, it is not possible to give a complete description of the ethmoid unit, although more

detailed information is available than for most other described osteolepiforms.

Prenasal Fossae. (See Terminology.) These fossae are well exposed on three specimens, QMF21083, 21104 and 21110, and are mesial and partly anterior to the nasal capsules (Figs 20A; 21A,C; 22; 25D). On QMF21110, the endocranial ridge is worn through to expose a mass of vesicular tissue, thereby demonstrating its endochondral origin (Fig. 21C). Anteriorly, the ventral edge of the endocranium is overlapped by a concave flange of the premaxilla (see below), which continues laterally to the articulation with the vomer; Jarvik (1966: fig. 17) referred to this structure in *Megalichthys* as the palatal lamina of the ethmoid shield. It lies directly on the endocranium, which in turn forms the roof and walls of the prenasal fossa. The posterior wall of the fossa is steep and terminates beneath the vomer. There is no suture in the endocranial bone of this wall as was shown by Jarvik (1966: figs 17A; 19D) for *Megalichthys*.

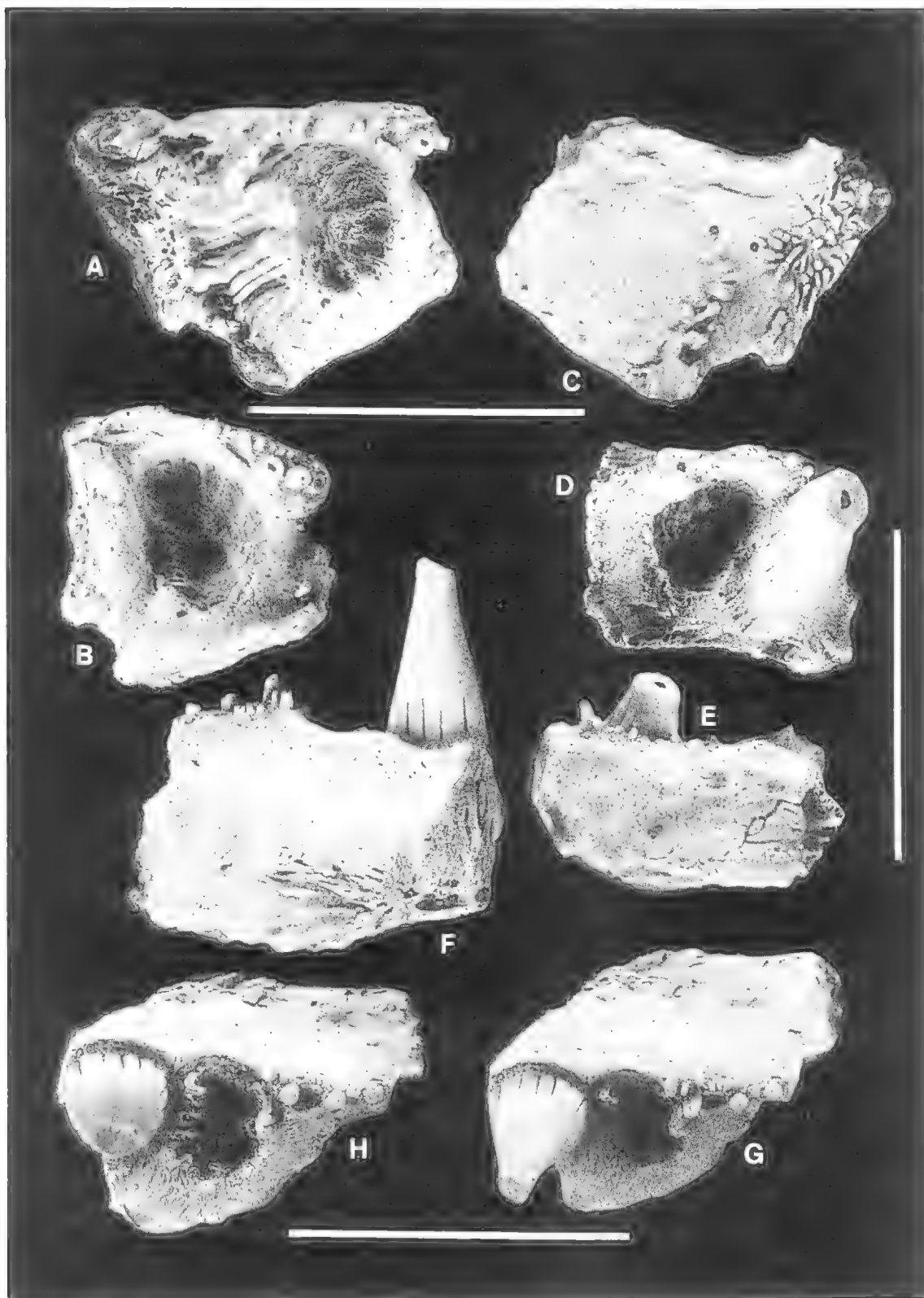
Several specimens of *Cladarosymblema* are well enough preserved to show that the prenasal fossa is in direct communication with the nasal capsule lateral to it. In QMF21104, a wide nasobasal canal (see below) penetrates the bony wall between the two, from the lateral extremity of the fossa to the base of the mesial wall of the capsule (Figs 20A; 22; 24; 25D); thereafter, the canal is continued part way across the ossified part of the floor of the capsule as a groove. In QMF21083, the canal has not been cleared of matrix, but foramina mark its course; however, these are substantially smaller, and the canal presumably narrower, than in QMF21104. Across the roof of the prenasal fossa in QMF21104 and 21110, a deep groove extends mesially from the lateral foramen and opens into two or more foramina that in turn open into the vesicular tissue making up the substance of the endocranium (Figs 20A; 21C). QMF21083 shows a much shallower groove on the left side and even less on the right, but several small foramina penetrate the bone here, as well. In the posteromesial corner of the prenasal fossa on QMF21104, there are two more foramina opening posteriorly into the vesicular tissue of the endocranium. We see no evi-

dence that these small foramina are interconnected or that their pattern is constant.

In *Megalichthys* and *Eusthenopteron*, the passage between the prenasal fossa and the nasal capsule was named the ventral branch of the nasobasal canal by Jarvik (1966: 86 & fig. 17). He believed it carried the medial branch of the profundus nerve, which then anastomosed with the palatine nerve. We can see no evidence that reflects the pattern of these nerves in this region in *Cladarosymblema*, and note that the basis for his interpretation is the presence of such an arrangement in the anuran *Rana esculenta*. Thomson (1964b: 326-7 & 345) has discussed this matter and has concluded that the nasobasal canal carried the ramus medialis narium of the profundus nerve. As noted above, the groove in the nasal capsule entering the nasobasal canal in *Cladarosymblema* runs below the olfactory bulb, whereas the profundus nerve passes above it (see below). Therefore, we accept the conclusions of neither Jarvik nor Thomson. Instead, we believe that a vein draining the prenasal fossa entered the corner of the nasal capsule and ran across its floor, an inference that is consistent with the marked individual variation that the channel and foramina show in the specimens of *Cladarosymblema*.

Jarvik (1966) claimed that the prenasal pit (presumably the deepest part of the prenasal fossa in our terminology) in *Megalichthys* contained an intermaxillary gland. From the vessels or nerves entering these spaces it may be inferred that some soft tissue was present, but we have no evidence to indicate what its dimensions or homologies might have been. Thomson (1964b:332) and Jarvik (1966: 83-84) have also suggested that in *M. hibberti* the anterior tusks of the dentary fitted into the prenasal fossae, but we have mandibles that are from animals of the same size as our ethmoid units, and these show that the tusks in question entered the fossae only shallowly and only on their anterior edges; most of the opening of the fossae would then have been opposed by the mandibular parasymphysial plate. However, during elevation of the lower jaw to full occlusion, the parasymphysial plate remained in too ventral a position to have entered the fossa, and its posterior (toothed) edge moved past the ante-

FIG. 18. *Cladarosymblema narrienense*. A-C, oblique, buccal and visceral views of incomplete right vomer, QMF26559. In A, note the lateral tusk is broken vertically to expose the labyrinthine structure. C shows the intricate modelling of the surface of attachment to the endocranium. D,E, buccal and anterior views of a broken left vomer, QMF26558. F-H, anterior and variously tilted buccal views of a right vomer, QMF26560. In F, note rugosities on the anterior face where the vomer fitted against the similarly patterned face of the premaxilla (see Fig. 25D). All specimens have the mesial projection broken off. Scale: 10mm.



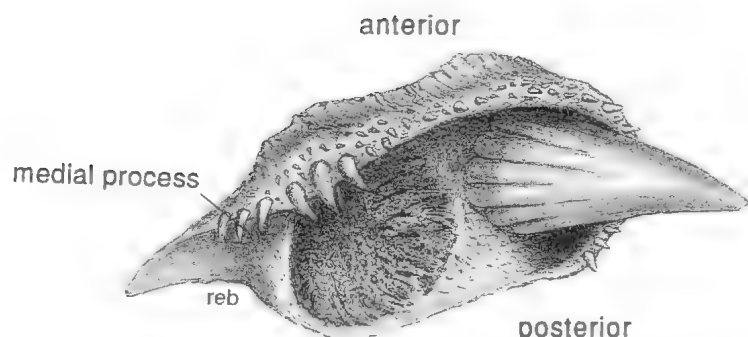


FIG. 19. *Cladarosymblema narrienense*. Reconstruction drawing of a vomer in oblique anteroventral view, based primarily on Fig. 18F,G, with the continuation of the denticles around the lateral crest is based on Fig. 18D,E.

rior (toothed) edge of the vomer. The suggestion that the fossae contained soft bodies of considerable size cannot be ruled out on that account.

Nasal Capsule. The nasal capsules are well preserved on two specimens (QMF21083, 21104) and less completely preserved on three others (QMF21105, 21108, 21110) (Figs 20A, B; 21A,C; 22; 23B; 24B; 25C,D). As is usual in osteolepiforms, the capsules are open ventrally through a large unossified solum nasi, the original borders of which can be reconstructed from the specimens at hand. The rim of this opening is not all in the one plane, but rises to form a notch lateral to the autopalatine articulation, and a more profound notch at the lateral extremity of the solum nasi (Figs. 21A; 25C,D). In life, as discussed above, the vomers would have extended laterally at least to a level below part of the bony capsules as preserved in these specimens, but almost certainly there was a vertical gap between the upper surface of the vomer and the opposing capsule rim. However, in *Cladarosymblema*, the floor of the nasal capsule, the solum nasi, was not ossified, although in our best preserved specimen (QMF21083), endocranial bone does complete the lateral wall of the nasal capsule beneath the circumnarial bones. Further ventrally in the capsule, however, the lateral wall is not preserved and we do not know the full extent of ossification beyond the limits shown on this specimen.

The external naris opens into the wall of the nasal capsule anterolaterally; beneath the naris, the lateral wall of the capsule is swollen out beyond the plane of the naris, carrying the capsule laterally well past the limits of the vomer beneath, unlike Thomson's reconstructions of *Ectosteorhachis* and *Megalichthys* (Thomson,

1964a: fig. 3). This has important implications for the position of the choana, which, as we have discussed in relation to the anterior shape of the maxilla, must have been posterolateral to the vomer and anterior to the maxilla. The premaxilla and the bones around the external naris are firmly fixed to the neurocranium, and although the maxilla and the lachrymal abut against, and are not fused to the bones ante-

rior and dorsal to them, we see no evidence that the snout was kinetic on the cheek (cf. Rosen et al., 1981:191, 234).

Apart from the foramen for the nasobasal canal, which has been dealt with under *Prenasal Fossae* above, several large foramina can be seen in the mesial and posterior walls of the nasal capsule (Figs 23B; 24B). The largest is for the olfactory tract, and it opens high on the posteromedial wall just under the dermal bones. The second largest foramen, which is only about one quarter the size of the olfactory opening on whose dorsolateral side it lies, opens posteriorly into a short tube that emerges through the antorbital wall into the orbital chamber. On our best preserved specimen, QMF21083, this foramen joins a groove that runs across the roof of the nasal capsule and enters a foramen in its mesial wall; this latter foramen can be seen in turn to divide into two channels more deeply. A second specimen, QMF21104 (Figs 23A; 24A) in which the roof had been eroded away before burial, shows a foramen on each side of the capsule in the same place, but the course of the canal across the roof has been lost. However, a foramen in the mesial wall is preserved in QMF21104 and this shows that it enters a ramifying set of deeply buried tubes that run forward and downward toward the premaxilla (see above). Although we have been unable to establish the connection, it seems likely that these tubes opened into those described above, for example in QMF21111, running beneath the lateral line system and carrying fibres for ophthalmicus profundus V to innervate the snout as in *Gogonasus* (Long, 1985a: fig. 5). This is an unlikely course for a nasolachrymal duct, a point we

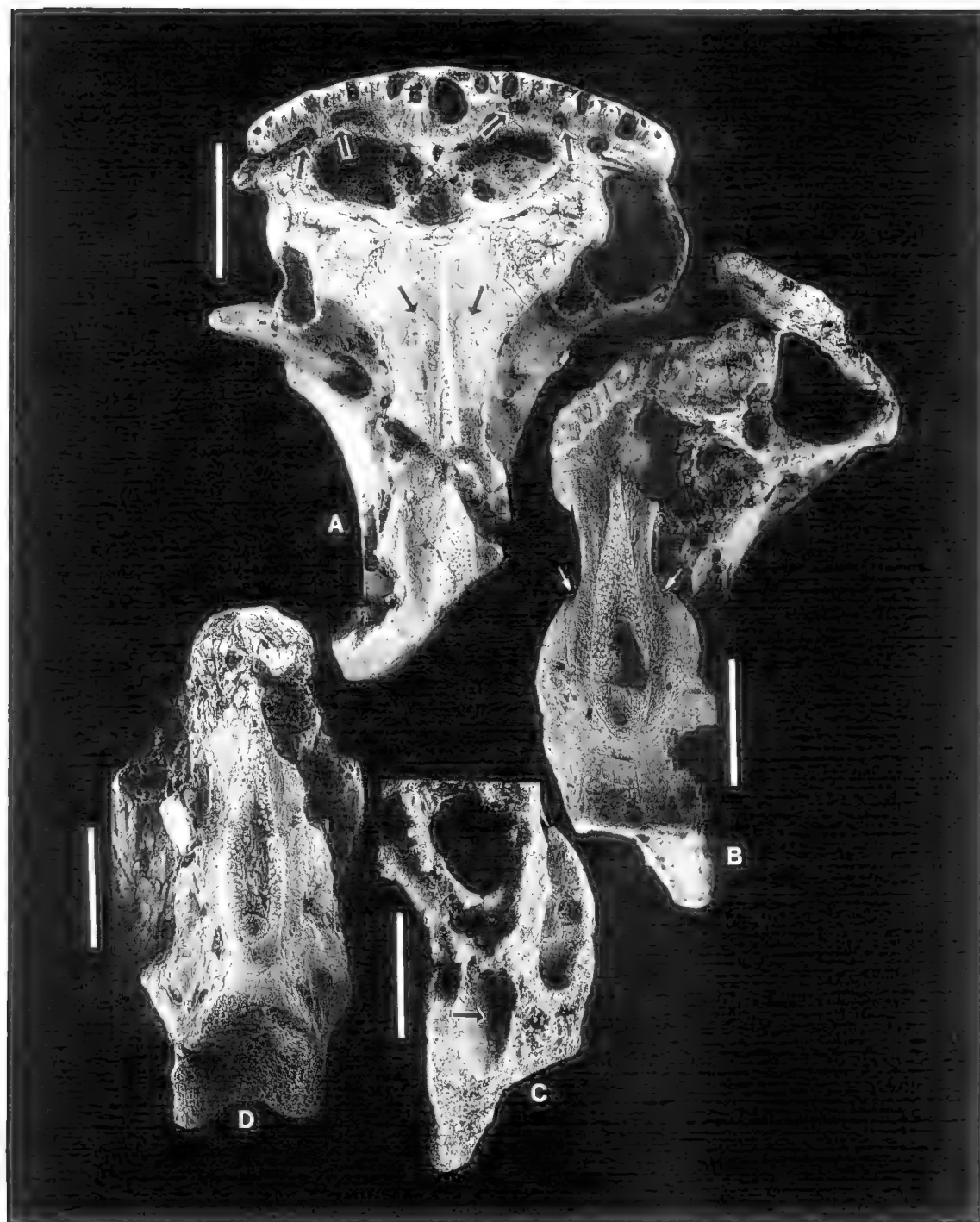


FIG. 20. *Cladarosymblema narrienense*. A, B, D, ventral views of three incomplete ethmoid units with parasphenoids attached, QMF21104, 21105 and 26547. In A, black arrows indicate anterior edge of parasphenoid; white bordered arrows indicate openings into the transverse (rostral) commissure of the lateral line canal. In B, arrows indicate position of notch. C, dorsal view of posterior part of the specimen in B showing hypophysial pouch (arrow). Scale: 10mm.

make because Jarvik considered that a large foramen in the ventrolateral part of the posterior wall of the nasal capsule in *Eusthenopteron*, carried a nasolachrymal duct. No foramen corresponding with this foramen of Jarvik occurs in *Cladarosymblema*, nor indeed in *Gogonasus*.

Other foramina enter the mesial wall of the nasal capsule in *Cladarosymblema*. In QMF21104, a groove passes up from the edge of the solum nasi ventrolateral to the olfactory foramen, curves around the ventral edge of that foramen, and leaves the capsule through a foramen (fm₁ in Fig. 24B) in the mesial wall just in front of the olfactory foramen. We do not know the function of this groove. Other minor foramina are present in this wall, but they are not consistently developed on even the two sides of a single specimen; nor are they constant between specimens. We consider these to be nutrient foramina. Specimen QMF21104 shows a small foramen in the posterolateral wall on both sides of the specimen, although it is largely eroded on the left. This enters a canal that opens high on the lateral extremity of the antorbital wall. No other specimen has this part of the animal preserved so that we cannot assess its significance. Its size and position suggest that it is more likely to have transmitted a nerve than a vessel, but apart from that comment we cannot offer any useful suggestion.

On QMF21083, a second large foramen penetrates the antorbital wall posterodorsal to the ophthalmicus profundus V foramen (Figs 21A; 22; 25D), but it does not open into the nasal capsule. Rather it opens into a tube that cannot be traced with clarity; however, what is clear is that it does not open into the same canal as the ophthalmicus profundus V. It runs mesially, and probably ramifies in the vesicular tissue between the olfactory canals. Such an orientation suggests the ramus ophthalmicus superficialis VII nerve. The foramen in question has been lost by erosion in QMF21104.

On QMF21083 and 21105 a smaller foramen occurs in the antorbital wall lateral to the foramen for the ophthalmicus profundus V (Figs 21A; 22). From it a tube passes through into the posterolateral corner of the nasal capsule where there is a conspicuous foramen. On QMF21083, a shallow groove runs up across the roof of the capsule parallel with the inner margin of the striated bone forming the inner surface of the bones surrounding the external naris. It passes over the top of the olfactory foramen and joins the same foramen in the mesial wall of the capsule as the ophthalmicus

profundus V. This groove is present on QMF21105 also, but the roof of the capsule has not been preserved so its course cannot be traced throughout. What occupied these foramina and groove? Thomson (1964b: fig. 3) considered that in *Ectosteorhachis* a lateral nasal vein exited the nasal capsule posteriorly in approximately the same position as the structure under discussion, but the more anterior course of the lateral nasal vein is around the flank of the capsule rather than over the roof and into the internasal septum as in *Cladarosymblema*. Hence, this is not an adequate interpretation. A second possibility is that it carried a ramus of nerve V, either the maxillaris or infraorbitalis (Jarvik, 1942: 477; Thomson, 1964b: 328). We prefer this interpretation because the groove across the roof of the capsule reaches the foramen we have interpreted as carrying the ramus profundus V. We have labelled it maxillaris N V in Fig. 22.

We have not dealt with the drainage of blood from the nasal capsule, because no foramina likely to have carried veins have been observed. It seems most likely that a vein passed out of the capsule into the lateral head vein through the notch near the autopalatine articulation.

Olfactory Canals. The olfactory canals are well exposed on QMF21104, in which the dermal roof has been eroded away (Fig. 23A); their disposition can also be inferred from QMF21083 (see also Fig. 28B). The separate canals arise towards the posterior end of the unit, much further posteriorly than in *Eusthenopteron* (e.g., see Jarvik, 1980: fig. 89), but are comparable in their pattern with those in *Ectosteorhachis* (see Romer, 1937: figs. 8,9). A short distance along their course, the canal for the optic nerve is given off in an anteroventrolateral direction (Figs 23A; 24A). This peculiar arrangement is matched by that in *Ectosteorhachis* as figured by Romer (1937: figs 8, 9). Further forward are several foramina of varying aperture in the floor of the olfactory canal (Figs 23A; 24A). These seem to connect with tubules that traverse the spongy tissue between the canals, but they seem not to exit the bone at any identifiable points more ventrally. Presumably they carried sensory nerves or vessels of some kind. Thomson (1964b: 321) has commented that cutaneous and ethmoid arteries passed through foramina in the walls of the olfactory tract; we are unable to comment further on the basis of our material. It is not uncommon to find such tubules in other osteolepiforms or in dipnoan specimens that are sufficiently well preserved to show them.

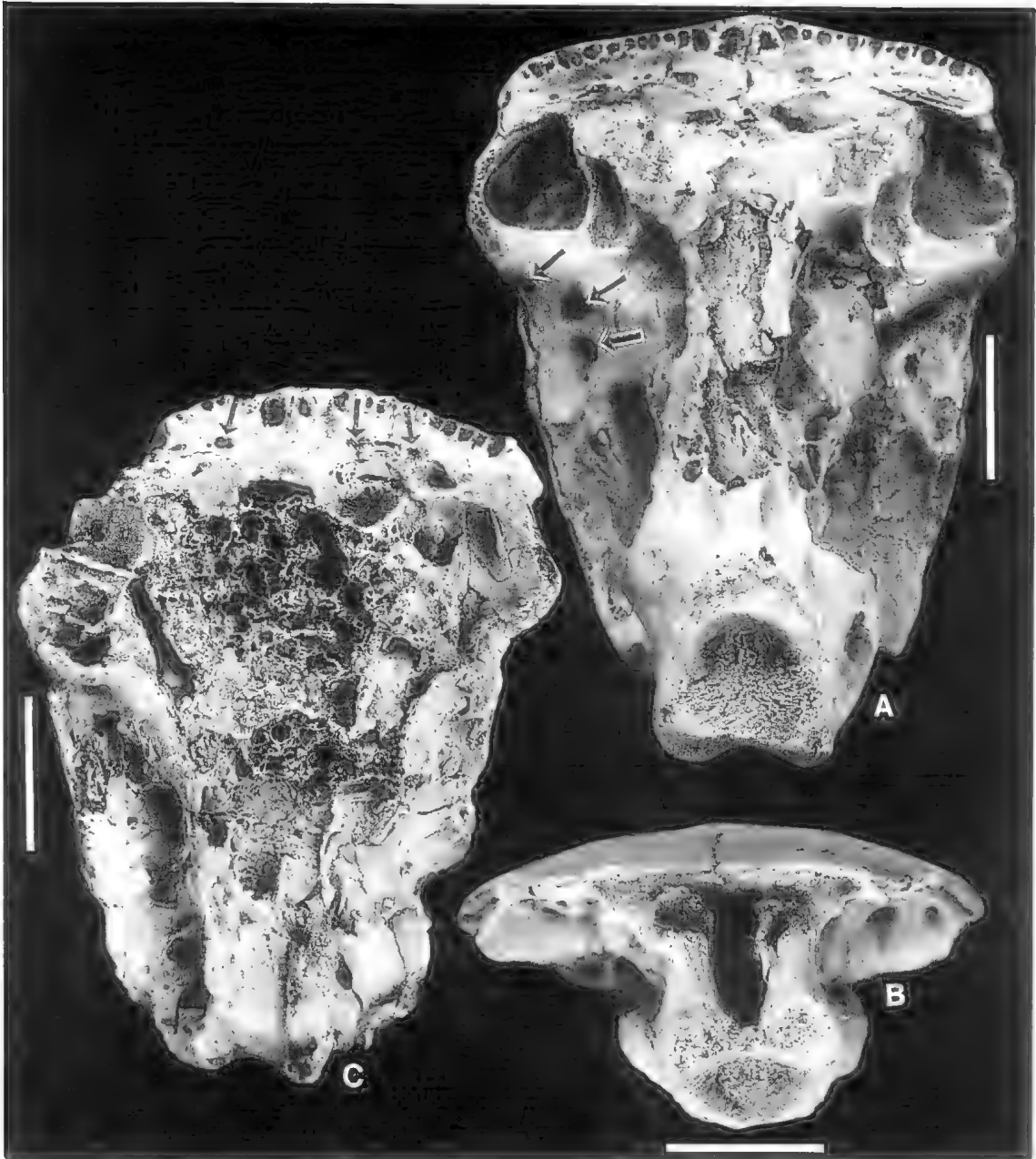


FIG. 21. *Cladarosymblema narrienense*. A-B, ventral and posterior views of QMF21083. The black arrows on the left side of Fig. A indicate (from left to right) the foramina for the maxillaris V, the ophthalmicus profundus V, and the ophthalmicus facialis VII. C, ventral view of incomplete ethmoid unit, QMF21110, showing spongiform tissue between the olfactory canals, openings into the transverse commissure of the lateral line canal (arrows), and the roof of the left nasal capsule. Scale: 10mm.

Inner Wall of the Orbital Chamber. The endocranial surfaces forming the inner wall of the orbital chamber are well preserved on QMF21083 and 21104, although on neither specimen are these surfaces complete. The wall stands

vertically under the roof, is swollen where it covers the olfactory canals, and is deeply concave more ventrally, forming a broad sub-olfactory recess (Figs 21A; 22) and meeting the lateral edge of the subocular shelf (=suborbital ledge of

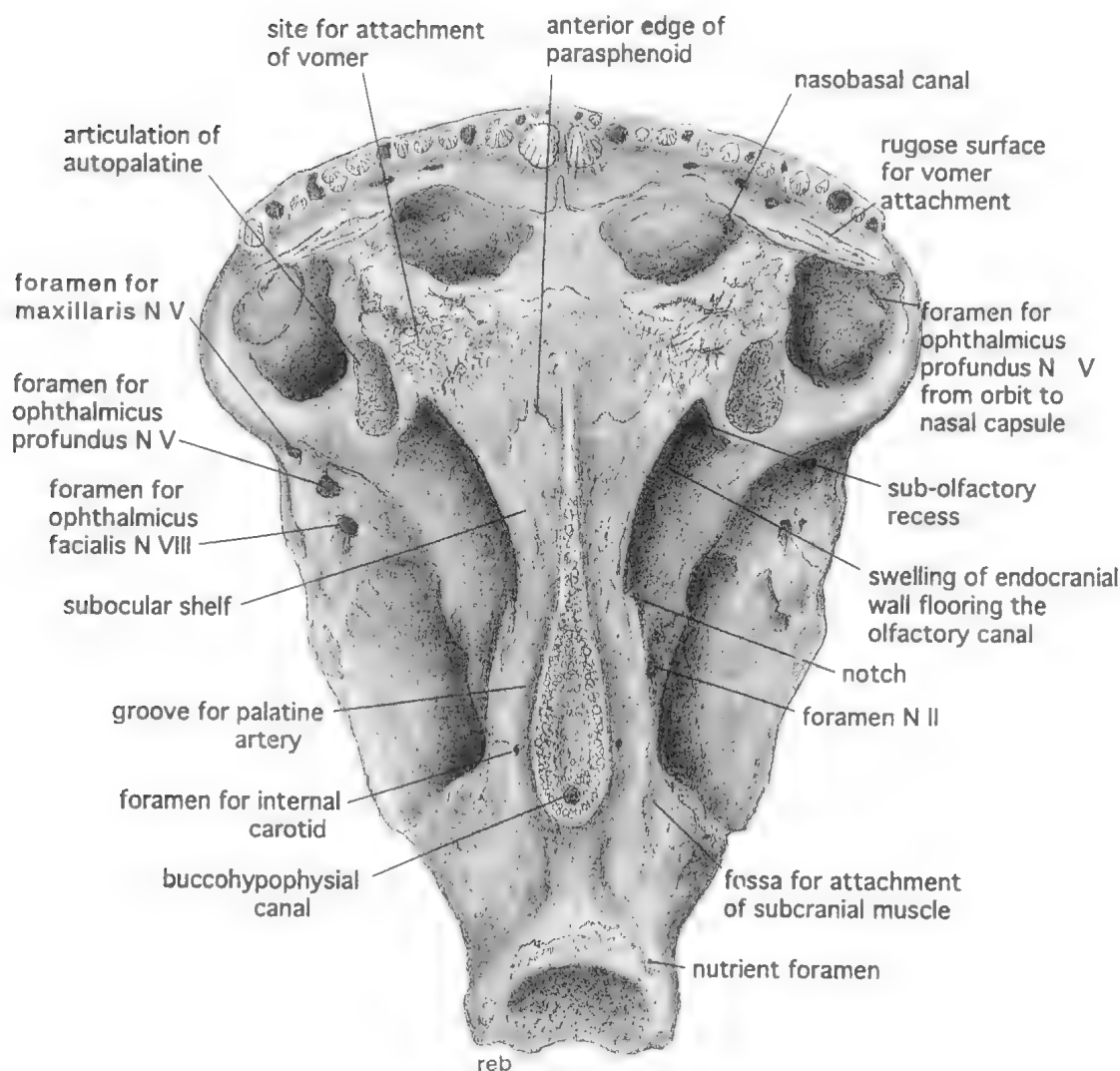


FIG. 22. *Cladarosymblemanarrienense*. Reconstruction of the ethmoid unit without vomers, based on QMF21083 and 21104.

Jarvik, 1980: fig. 86A) along a sharp keel; the ventromesial edge of the pterygoquadrate articulated in this recess.

Anteriorly, and immediately below the nasal capsule, is a deeply concave facet of vesicular bone (Figs 20A; 21A; 22; 25D) that received the anteromedial process (pars autopalatina) of the palatoquadrate. This facet extends far enough ventrally to border upon the horizontal attachment surface for the vomer, and it terminates

posterodorsally at the base of the antorbital wall. This articulating surface is twisted, with its anteromesial extremity directed laterally and its posterior extremity facing ventrally. In life, presumably, it was lined with cartilage, and the complexity of its surface is probably related to limiting the range of possible movement of the pterygoquadrate on the endocranium.

Posteriorly from the autopalatine facet, the sub-olfactory recess is the dominant feature of the

lower parts of the endocranial wall, and this recess becomes progressively deeper posteriorly; its surfaces are marked by irregular processes, ridges and depressions that reflect the connective tissue attachments of the pterygoquadrate to the endocranial wall. The recess terminates at a laterally robust process (Figs 20A-C; 21A; 22) that is mostly formed by endocranial bone but is sheathed superficially by the parasphenoid (see below). This structure is the basipterygoid process, the site of the second, and perhaps the most important moveable joint between the pterygoquadrate and the endocranium. In *Cladarosymblema*, the basipterygoid attachment is C-shaped in lateral aspect, with the ventral arm of the 'C' prolonged anteriorly. The articular surface of the process consists of vesicular bone that lacks a perichondral covering. Most posteriorly, where the process is especially robust, this surface is nearly vertical and faces anteriorly. As it continues ventrally and then anteriorly, along the ventral arm of the 'C', the articular surface comes to face increasingly laterally. Directly above the basipterygoid process, just beneath the skull roof on QMF21083, is a small patch of unfinished bone that may represent the suprapterygoid process, the third site of attachment of the pterygoid on the endocranium. Jarvik (1980: fig. 8) has illustrated a suprapterygoid process in this position in *Eusthenopteron* and Long (1985a: fig. 3) in *Gogonasmus*.

Anteriorly, the basipterygoid process encloses a pit (Fig. 25A, black arrow), deep within the confines of the 'C'; this pit in *Eusthenopteron* was interpreted by Jarvik (1980: fig. 85) as being for the retractor bulbi muscle, a muscle found in tetrapods and used for pulling the eye deeper into its socket. The evidence for this is not clear. On the other hand it would be appropriately placed with respect to the line of muscle action and the position of nerve III to be the myodome for the posterior rectus eye muscle in a fish. Long (1985a: fig. 3B) reached the same conclusion with respect to *Gogonasmus andrewsae*. At the base of the pit is a foramen for the exit of the pituitary vein; the vein must then have continued dorsally to join with the jugular vein; the passage posteriorly of the latter is marked by a shallow groove (Fig. 25A) above the basipterygoid process (QMF21008, 26547). The scars for the attachment of the other eye muscles have not been positively identified.

In *Cladarosymblema*, the optic nerve foramen is a major landmark on the orbital wall (Fig. 25A-D). It opens on the olfactory ridge a short

distance anterior to the basipterygoid process. It is large and ovate, and the optic canal for passage of the nerve from the endocranium is oriented anteroventrally and leaves the olfactory tube near its base (see above). Nerve III exited from the endocranium via a small foramen posterodorsally adjacent to the optic foramen (Fig. 25A), as shown in QMF21083, 21104, and 26547, a position similar to that in *Eusthenopteron* (Jarvik, 1980: fig. 86) and *Gogonasmus* (Long, 1985a: fig. 3). Romer (1937) and Thomson (1967) were unable to recognize the foramina for nerve III and IV in *Ectosteorhachis*; and we have been unable to recognize the foramen for nerve IV in *Cladarosymblema*.

Immediately anterior to the optic nerve foramen on both sides of QMF21104 is a small sub-circular scar about 1mm in diameter that has a slightly raised periosteal rim (Fig. 25B,C; asterisk). A similar scar occurs in *Gogonasmus* (ANU 49259) as well; consequently, there can be no doubt about its anatomical reality. Obviously, soft tissue of restricted extent was attached to it. The only possible eye muscles to attach at such a point would be the obliques, but in our view the scar is unlike a muscle attachment and is not appropriately placed to be so interpreted (Goodrich, 1958: fig. 244). An alternative explanation would be that this structure represents an eye stalk such as occurs in elasmobranchs and placoderms. According to Young (1986: 15), however, the eye stalk is 'similarly positioned in both groups, behind the optic nerve and beneath the oculomotor foramen'. In our material the scar is clearly anterior to the optic nerve, and hence this option is also ruled out. Furthermore, as far as we are aware, an optic stalk has not been previously recorded in osteolepiforms, nor in any other sarcopterygians.

Above the optic foramen in *Cladarosymblema*, the endocranial wall appears to have been depressed mesially, forming an elongate fossa beneath the skull roof. The exact dimensions of the fossa cannot be determined owing to breakage and erosion. Long (1985a) identified a fossa in this position in *Gogonasmus* as serving as the attachment area for arcus palatini muscles. A similar interpretation for the area is warranted in *Cladarosymblema*.

Base of the Endocranium. Posterior to the prenasal fossae, the endocranial surface is broad and flat, and is marked by an irregular pattern of ridges and furrows, the sites of attachment of the vomers. These sites are broad and extend laterally over the endocranial surfaces that encroach on the



FIG. 23. *Cladarosymblema narrienense*. A, dorsal view of a fragment of ethmoid unit, QMF21104, with most of the roof eroded away exposing olfactory tracts and nasal capsules. Anterior parts of lateral line canals excavated to show their great depth of burial. B, anterolateral view into the right nasal cavity of the same specimen. Large opening is the olfactory tract. For interpretation see Fig. 24B. C, posterodorsal view of QMF26547 showing parietals and large median postrostral. Posterior part of the roof has been eroded to allow a view into the hypophysial pouch (arrow). Scale: 10mm.

outline of the nasal capsule (Figs 20A; 21A; 22). Mesially, the markings fade and on QMF21083, they are quite obscure. They include a complex network of vascular elements that may have supplied the vomers and the connective tissues that held the vomers in place. On QMF21104, the rugosities are sufficiently clear to show that the vomers extended to, or almost to, the midline.

Posterior to the vomerine attachment surfaces, the base of the endocranium narrows to a level

just anterior to the vertical plane containing the optic foramen, behind which it widens posteriorly to the basiptyergoid attachment. Ventrally, QMF21105 shows a notch (Figs 20B; 22: notch) on both edges of the parasphenoid, about midway along the length of the subocular shelf; a short groove leads to the notch from the posterior. This specimen is the only one in our collection that is undamaged in this area, but QMF26547 shows evidence that it had similar structures. As far as

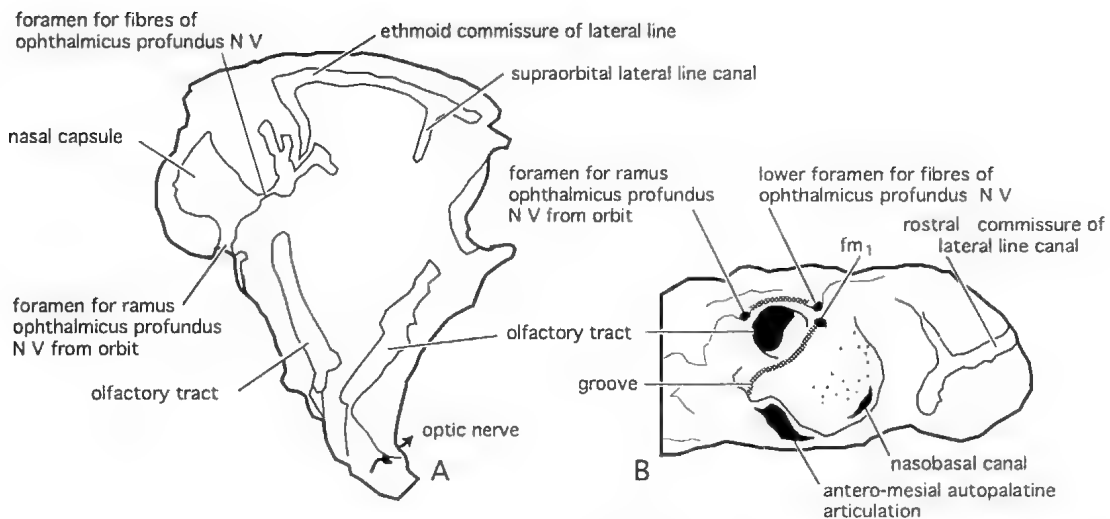


FIG. 24. Labelled outline drawings of Fig. 23A,B.

we are aware, no structure resembling this notch has been reported in other osteolepiforms, but a comparable structure occurs in the specimen of *Megalichthys* used by Jarvik (1966: fig. 17A & pl. 3), and in *Gogonasus* (ANU49259), in which it is much closer to the foramen for the palatal artery. The notch marks the passage of a nerve or vessel dorsally, to a level above the lateral flange of the parasphenoid, and then on to tissues between the endocranial wall and the opposing surface of the pterygoquadrate. Although it cannot be proved, it seems likely that the notch would have carried a branch of the palatine artery. (See below for a discussion of this vessel.)

Posterior Part of the Endocranium of the Ethmoid Unit. As is shown particularly well by QMF26547, on either side of the denticulated surface of the parasphenoid anterolateral to the buccohypophysial foramen, the internal carotid artery enters the basicranium through a moderate-sized foramen (Fig. 22). Posterior to this foramen is a shallow groove that runs from near the base of the basipterygoid attachment, where it disappears from the surface of the bone. It marks the course of the internal carotid artery. Closely associated with the internal carotid foramen is a slit-like furrow for the palatine artery, which leaves the basicranium to continue further anteriorly in a shallow groove. This slit-like furrow is partly concealed on the right side of QMF26547 by a small ventral shelf, but this is probably of little consequence as it is not present on the left side. Thomson (1964b: fig. 7) has figured a similar arrangement of the internal carotid and pala-

tine arteries for *Ectosteorhachis* and Jarvik (1966) has noted it for *Megalichthys*. The only other specimen sufficiently well preserved to show this area is QMF21105, but it has not preserved these foramina. On the other hand, QMF21083 and 21104 show short vertical openings in this position, apparently reaching up into the base of the hypophysial pouch, as would be expected if this were the position of the internal carotid.

On each side of the same specimen, near the base of the basipterygoid process, is a foramen in approximately the same position as the one regarded by Romer (1937: fig. 4) as carrying the internal carotid in *E. nitidus*. Each is entered from a posterolateral direction by a short groove. We agree with Jarvik (1966: 91-92) that these foramina have been incorrectly identified by Romer, and are nutritive foramina associated with the attachment of the subcranial muscles. The scars for these muscles are well preserved on QMF21083 and 36547 (Figs 20D; 22). The posterior part of the endocranium of the ethmoid unit is constructed in its entirety of robust but finely vesicular endochondral bone covered by a well-developed perichondral layer.

The anterior end of the notochord fitted within a shallow, rounded pit (Figs 21A,B; 22), as in *Ectosteorhachis* and *Megalichthys* (see, e.g., Romer, 1937; Jarvik, 1966). In *Cladrosymblema*, this pit has a sharply defined rim around its ventral and lateral sides (see QMF21083, 26547), although the ventral edge has been eroded in QMF21083. Poster-odorsally to the edge of the notochordal pit are the scars of the processus connectens, marking the ventral

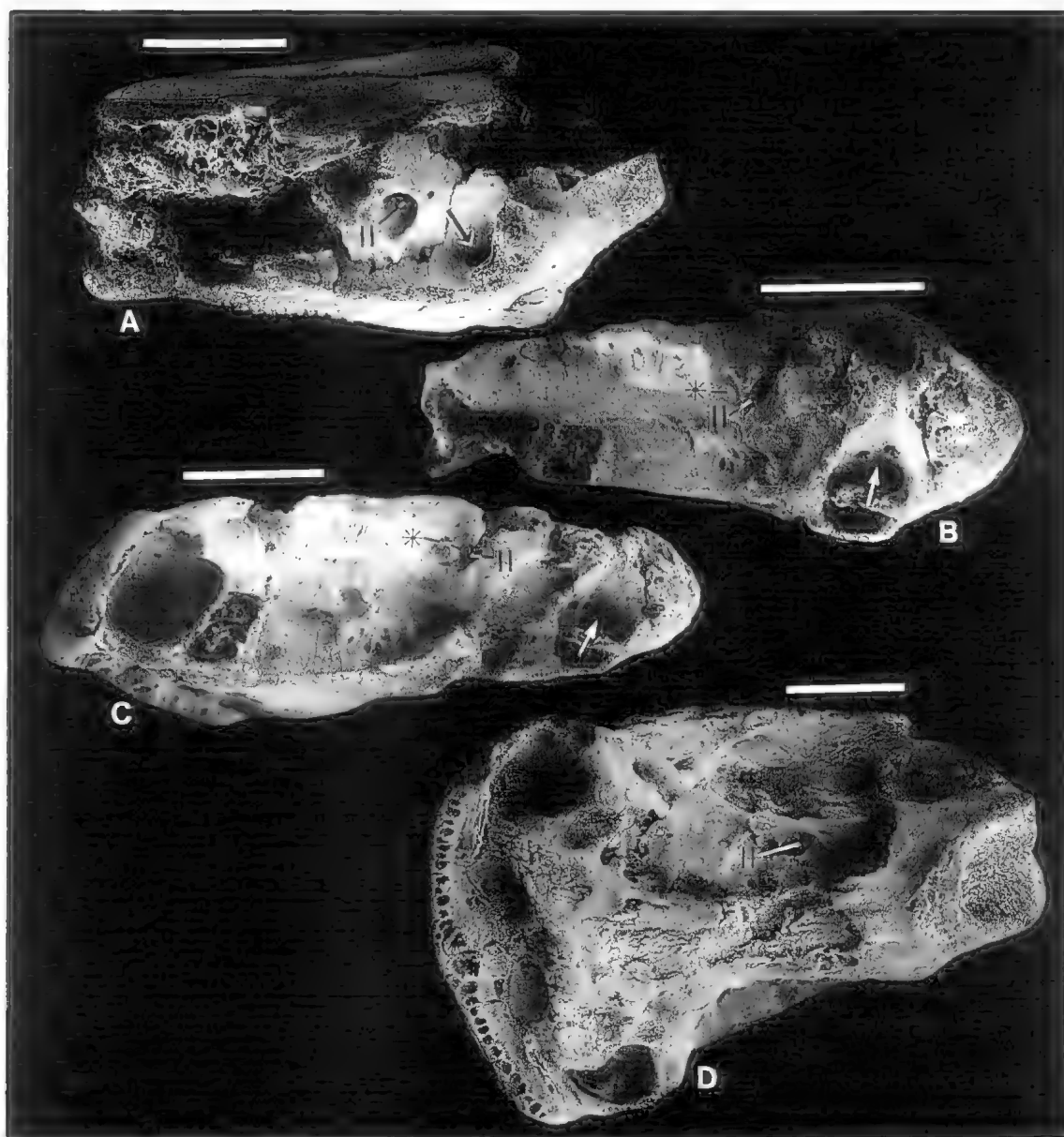


FIG. 25. *Cladarosymblema narrienense*. All figures are of ethmoid units. A, lateral view of QMF26547 showing large foramen for the optic nerve II, small foramen for the oculomotor nerve III posterodorsal to it, and a large myodome with foramen for the pituitary vein posteroventral to it (arrow). Spongiform tissue occupies the anteromesial space between olfactory tracts. B,C, two lateral views of QMF21104 with specimen tilted at different angles to show details of the hypophysial fossa (white arrows), and foramina opening into its anterior and lateral walls. Note the gap between the base of the hypophysial pouch and the buccal surface of the parasphenoid, and the foramina in the walls of the pouch described in the text (see Fig. 26). Asterisk indicates scar for a stalk of unknown function. D, oblique ventral view of incomplete ethmoid unit, QMF21083. Optic nerve foramen labelled II. Scale: 10mm.

articulation of the endocranium of the ethmoidal unit with that of the otico-occipital unit. The anterior ascending process of the parasphenoid

(see Jarvik, 1980: 172) covers the side of this bone, and is depressed relative to the most lateral extent of the processus connectens, but we see no

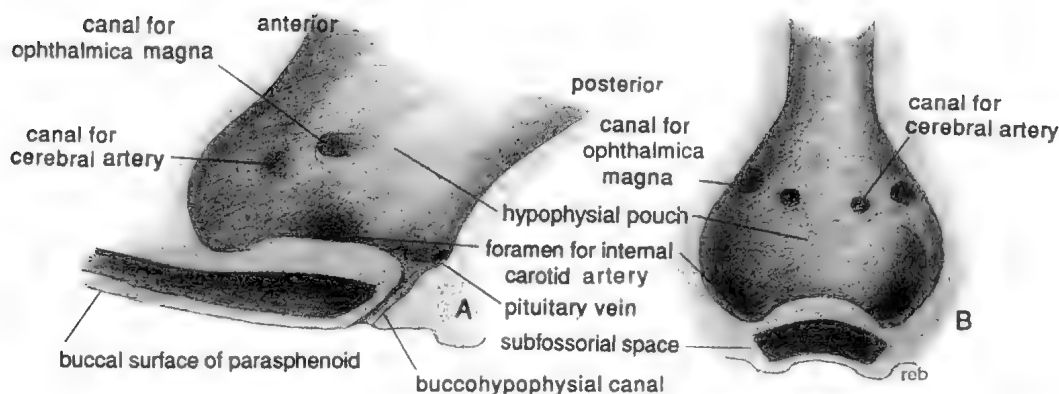


FIG. 26. *Cladarosymblema narrienense*. Reconstruction drawing of the hypophysial pouch and its foramina, based on the specimen in Fig. 25 B,C.

anatomically distinct structure here reflecting what Jarvik (1980: 172) has identified as the prespiracular groove in *Eusthenopteron*.

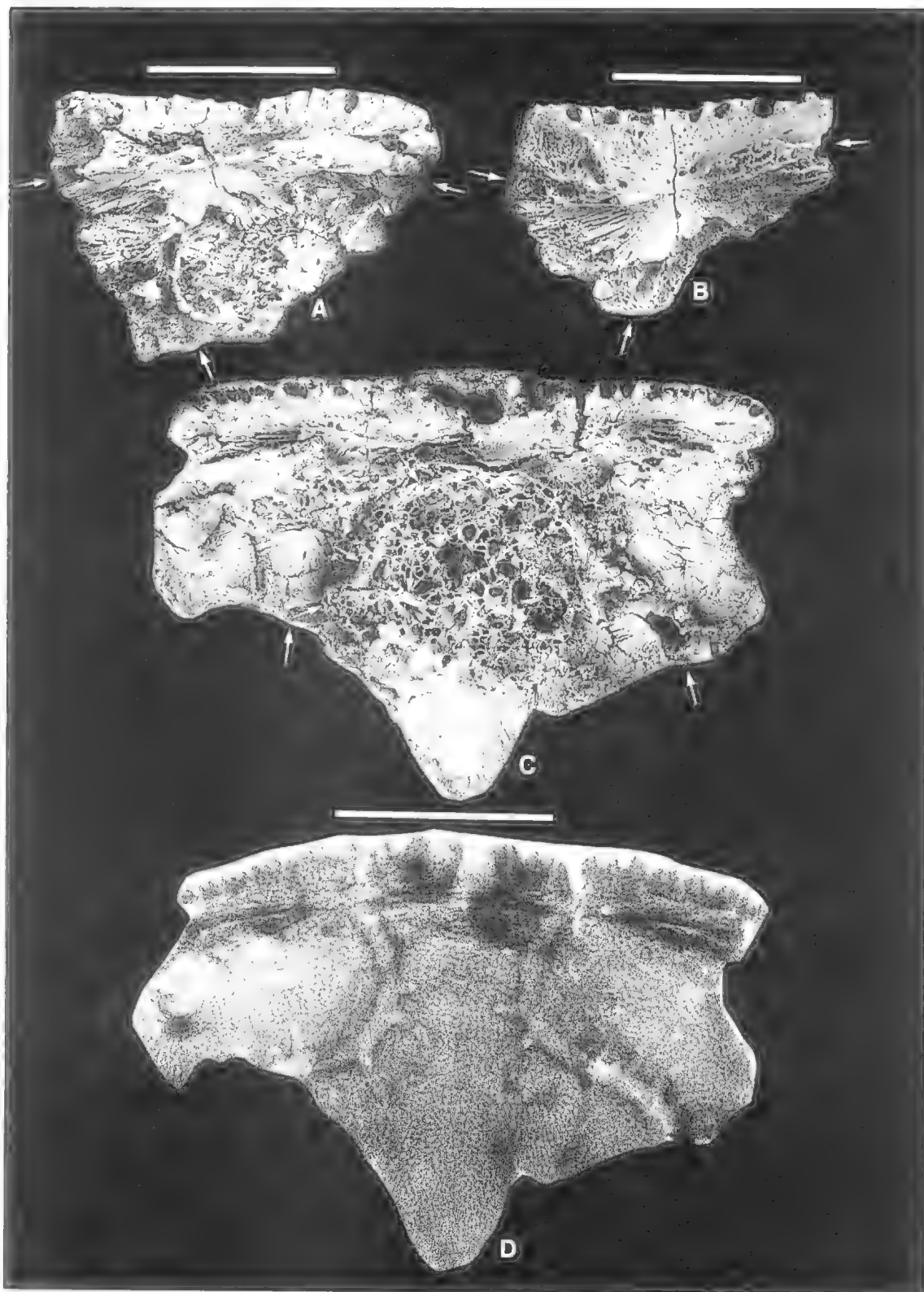
Above the notochordal pit is the cavity for the brain stem; it has a thick floor and lateral walls. Ventrally, the posterior edges of these walls, which face the posterior unit, are vertical, but more dorsally they are inclined anteriorly at a steep angle. The external surfaces of the bone here have been damaged on even our best-preserved specimens, but they retain evidence of ligaments that extended between the two units and held them together. At their dorsal ends, the posterior braincase walls flare laterally and are fused to the ventral surface of the parietals (Fig. 21B). Along their outer edges, immediately beneath the parietals, they contain deep vertically striated pits for the articulation of the supratemporal process (the fronto-dermosphenotic process of Bjerring, 1972). Below these is the small patch of vesicular bone forming the supraterygoid process for the distal articulation of the pterygoquadrate. This is well-preserved only on QMF21083.

Hypophysial Fossa. The best specimen for examining the hypophysial fossa is QMF21104 (Fig. 25B,C), which exposes the right side and most of the front wall. The fossa and the buccohypophysial opening (see above) are preserved on QMF21105 and 26547, but do not expose as much detail. Putting together the data from all these specimens (Fig. 26), it is clear that the fossa emerges from the floor of the cranial cavity near the posterior end of the parasphenoid. The dorsal part of the fossa is elongate and narrow (Fig. 20C), and it passes down into a large flat-bottomed chamber that is subtriangular in trans-

verse section. The anterior wall of the chamber is planar and its lateral wall concave. The internal carotid artery joins the fossa at its anterolateral corner through a passage that runs posteromedially from its external opening on the palate. A pair of foramina opens half way up the anterior wall of the fossa, one on each side of the midline. A second foramen opens in the anterolateral angle of the chamber dorsolateral to the one previously mentioned. These mark canals that appear to run anteriorly and anterolaterally from the fossa. In *Gogonasus* (ANU49259), a foramen opens externally a short distance anteriorly from the hypophysial fossa in the appropriate position for the exit of this laterally placed canal, and we assume a similar arrangement in *Cladarosymblema*, although the specimen is not well enough preserved to show the external foramen. In *Eusthenopteron*, Jarvik (1980: 118) has interpreted a tube in this position as having carried the ophthalmica magna artery supplying the soft tissues dorsal to the palate. The more mesially placed canal is likely to have transmitted the cerebral artery. Posteriorly, on the broken lateral wall of the fossa in QMF21104 (Fig. 25B) is the incomplete rim of a foramen that marks the exit of the pituitary vein.

QMF21105 and 26547 show the buccohypophysial canal best among the specimens at hand (Fig. 20B,D). It leaves the floor of the fossa a short distance behind the anterior wall and runs in an anteroventral direction to open about 1 mm in front of the posteriormost edge of the denticulated area of the parasphenoid.

The pattern of the whole hypophysial fossa seems very different from that of *Eusthenopteron* (Jarvik, 1980: fig. 196B), which genus should not be taken as representative of the condition in



osteolepiforms. The structure seems to be highly variable within the group. It is also very different from that of the porolepiform *Glyptolepis* figured by Jarvik (1980: fig. 196A).

OTICO-OCCIPITAL ENDOCRANIUM

Occipital Region. No specimen having this part of the skull preserved is uncrushed or otherwise undamaged, but we nevertheless have five specimens that yield important information (QMF21084, 21085, 21094, 21096, 21109); of these, QMF21085 and 21094 are the most useful. In those specimens, the occiput extends well behind the postparietals and the endocranium is well-ossified in this region. It forms a flat platform (the occipital shelf) that continues backwards from the posterior edge of the postparietals and that supported the anterior parts of the extrascapular series (Figs 38A,B; 39A,B). This shelf narrows laterally and does not extend fully to the lateral extremity of the postparietals. At its lateral limit, a separate shelf of dermal bone is developed by the tabular. It is separated from the neurocranial shelf by a notch (Fig. 38B) that is situated beneath the most lateral extent of the postparietal.

On either side of the midline beneath the occipital shelf in QMF21094, a shallow but well-defined fossa lined with pitted and ridged bone is developed. This fossa appears to have been the area of origin for muscles and ligaments extending to the anterior vertebrae (Figs 38B; 39B). Anterior and lateral to this fossa is a much deeper depression that presumably also provided the origin for axial muscles and ligaments. The roof of this latter depression is penetrated by a large foramen that opens to the dorsal surface of the occipital shelf. This foramen opens into a vertical tube that is continuous with a broad groove that runs anterolaterally and turns beneath the postparietals, through foramina including several minor ones laterally (Figs 38A,B; 39A,B). These grooves and foramina seem most likely to have been associated with blood vessels. In *Eusthenopteron*, Jarvik (e.g., 1980) has identified a system of grooves in this region as carrying the

occipital artery and its branches forward across the endocranial roof of the otico-occipital unit. We have observed similar grooves in two large fragments of *Cladarosymblema* (Fig. 31A,B), but these are not sufficiently well exposed to enable us to outline their disposition. They were probably vascular in function, and probably connected with the occipital artery.

Mesial to the large foramina that penetrate the occipital shelf in *Cladarosymblema* is a pair of much smaller openings that clearly run forward into the endocranial cavity, well seen in QMF21094 and 21085 (Figs 38A,B; 39A,B); these openings represent the emergence of the endolymphatic duct from the skull (see below for evidence of the course of these ducts within the endocranial cavity). In *Latimeria*, the endolymphatic duct leaves the skull roof posteriorly and terminates beneath the extrascapulars (Millot & Anthony, 1958) and perhaps the duct had a similar configuration in *Cladarosymblema*, as would be indicated by QMF21094. Other specimens, however, have a somewhat different structure. In QMF21056, a smaller specimen than QMF21094, the occipital shelf is narrower and the posteriormost parts of the postparietals conceal the foramina for the occipital vessels and the endolymphatic ducts from dorsal view, making it even more unlikely that the ducts reached the body surface. In any case, these differences in proportions most probably are age-related and have no taxonomic significance.

In QMF21094 and 21085, a deep median pit passes forward between the openings for the endolymphatic ducts immediately beneath the dermal roof (Figs 38A,B; 39A,B). This pit corresponds to the attachment of the supraneural ligament in *Eusthenopteron*, as identified by Jarvik (1980: fig. 86).

The outer edge of the occiput in QMF21085, the best preserved of our specimens in this part of the skull, is bounded by a rounded ridge that encloses the posterior vertical semicircular canal; this ridge also forms the inner rim of the entrance to the fossa Bridgei, the major cavity in the skull for the origin of axial musculature. Just mesial to

FIG. 27. *Cladarosymblema narrienense*. A, a left premaxilla in ventral view, QMF26540, with some tectals attached, all showing distinct radiation centres. Arrows show transverse (rostral) commissure and anterior end of supraorbital lateral line. B, isolated left premaxilla, QMF31877, in ventral view; arrows show entry points of lateral line canals. C, Paired premaxillae and attached small polygonal roofing bones on each side, QMF21111, identified by their distinct radiation centres and in some instances by their sutural boundaries. Arrows show lateral line entry points. Note tubules embedded in spongiform tissue (inner white arrows). D, X-radiograph of the specimen shown in C. (This and subsequent X-radiographs have been made by printing X-ray negatives on hard photographic paper.) Scale: 10mm.

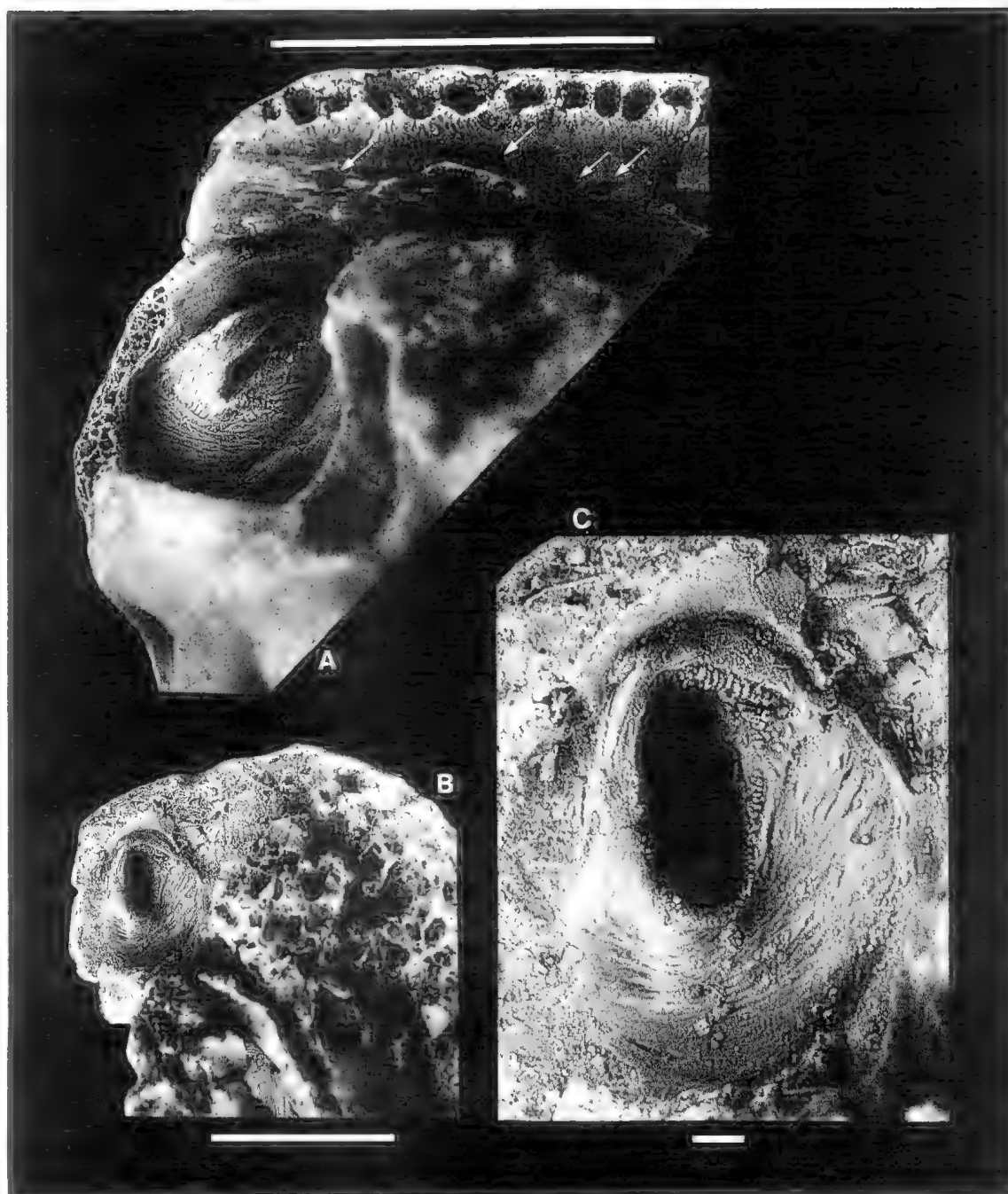


FIG. 28. *Cladarosymblema narrienense*. Ventral views into the nasal capsules of two specimens. A, right nasal capsule, QMF21083, showing the bones with characteristic texture forming the roof of the capsule, the eroded lateral edge of the capsule formed from thick vesicular endocranial bone, and a thin outer rim of dermal bone (see also Fig. 21A). Note behind the teeth in the premaxilla several pores that open into the transverse (rostral) commissure of the lateral line canal (white arrows). B, ventral view of right nasal capsule of an eroded specimen, QMF21108, showing the relationship of the capsule to the olfactory canal. C, enlargement of the roof of the nasal capsule in B. Note the mass of small denticles around the edge of the narial opening; especially well developed in the embayment on the mesial side. Scales: A, B, 10mm; C, 1mm.

the base of this ridge are two large foramina, one above the other, and separated by a slightly protruding lip (Figs 34A; 35A; 38A; 39A). They open externally at or near the junction between the occipital ossification and the auditory capsule. These foramina lead into short canals that pass through the braincase wall just posterior to the sacculus; within the wall, the canals join and open to the cranial cavity by a single foramen. From comparison with *Ectosteorhachis* (Romer, 1937:14), the lower foramen transmitted nerve X, and the upper, the posterior lateral line nerve. These two nerves are also closely associated, for example, in *Neoceratodus* (Northcutt, 1987), and have been reconstructed according to this same pattern in *Eusthenopteron* (Jarvik, 1980, fig. 86C). In *Gogonassus* (ANU49259), a fissure that incorporates the separate foramina opens here, and each foramen is subdivided at least once, indicating the exit of several at least partially separated trunks of these nerves.

Immediately below and slightly in advance of the vagus foramen in QMF21085, a subcircular depressed area is developed in which vesicular bone is exposed (Fig. 38A). This corresponds in position to the postotic process or facet for the attachment of the first suprapharyngeal branchial arch in *Eusthenopteron* (Jarvik, 1980: fig. 86) and in *Ectosteorhachis* (MCZ6499) (Thomson, 1967:229). In *Gogonassus* (ANU49259), a blunt process occupies this position; its surface lacks periosteal bone and probably articulated with the suprapharyngeal branchial, as well. In *Eusthenopteron*, the opening for cranial nerve IX is found below this facet. In none of our specimens of *Cladarosymblema* is this part of the skull well preserved, but QMF21085 retains what may be part of the rim of the foramen for nerve IX; nerve IX opens at this position in *Gogonassus*. In both QMF21085 and ANU49259, a system of ridges runs anteroventrally from the suprapharyngeal branchial articulation; their significance is unknown, but they possibly mark the attachment of various muscles, including the hyomandibular adductor, protractors of the first branchial arch, and a protractor and adductor of the opercular, as in *Ectosteorhachis* (Thomson, 1967: 229).

Fossa Bridgei. The fossa Bridgei in QMF21085 is a more or less pear-shaped space in cross-section, with its apex directed laterally and dorsal side flattened. In *Ectosteorhachis* (MCZ6499, Fig. 42A), the posterior entrance to the fossa is more nearly rectangular than in *Cladarosymblema* (Fig. 38A), with the lower rim subparallel to the upper. The mesial wall of the

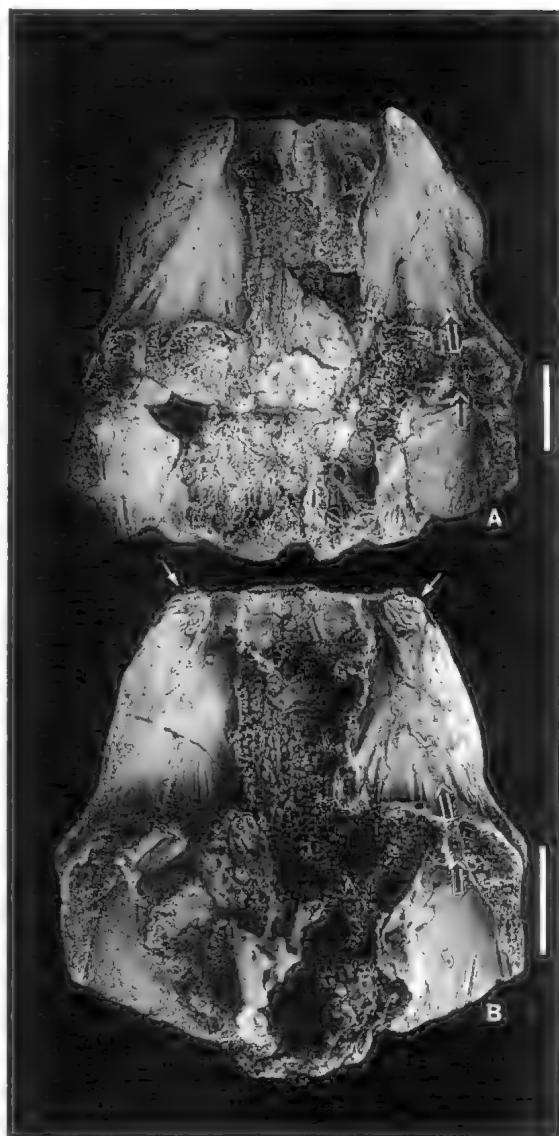


FIG. 29. *Cladarosymblema narrienense*. A,B, ventral views of the roofs of two otico-occipital units with most of the endocranium removed, QMF21086 and 21096. Note centres of radiation of the supratemporals and tabulars; transverse attachments of the endocranium to the postparietals, the tabulars, and the posterior extremity of the supratemporals; the longitudinal attachment of the endocranial walls to the postparietals; the almost complete restriction of the crista parotica to the ventral surface of the tabulars. Articulatory processes on the supratemporals have deep grooving (white arrows) and a slot on their dorsal edges for the articulation of the edge of ethmoid unit. The foramen for the occipital artery connecting the fossa Bridgei with the trigemino-facialis chamber indicated by black arrows. Scale: 10mm.

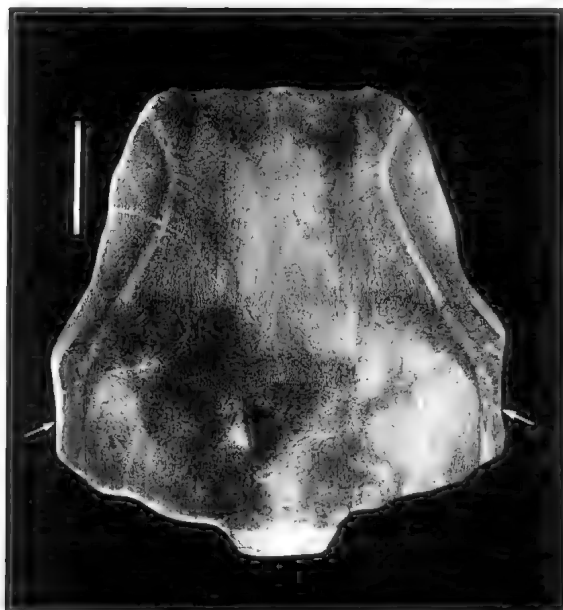


FIG. 30. *Cladarosymblema narrienense*. Roof of an otico-occipital unit, QMF21096 (see also Fig. 29B). Note lateral line canals, the absence of branches into the postparietal, the faint canals branching off into pores in the supratemporal, and the thick branch (arrows) on both sides into the putative extratemporal. Scale: 10mm.

fossa in our specimens consists partly of a continuous sheet, and partly of a meshwork of finely reticulated endocranial bone (Fig. 32C). Most of the roof of the fossa Bridgei, however, is of dermal bone, provided by the undersurface of the tabular and the most lateral extent of the postparietal, particularly well shown in QMF21086 and 21096 (Fig. 29A,B). At its anterior end, the fossa is nearly completely walled off by the endocranial bone that encloses the anterior vertical semicircular canal. However, in QMF21085, two foramina, one above the other, penetrate this wall, connecting it with the trigemino-facialis chamber anteriorly (Fig. 32A; arrows). In QMF21096 most of the endocranium has been removed, but the two foramina are still preserved on the left side, the more dorsal one being depressed (Fig. 29B). In QMF21084, there is only one large foramen at that location. The function of these foramina is uncertain. Romer (1937, fig. 5) showed a single large foramen (dorsomesial to a smaller foramen for nerve VII) in this position in *Ectosteorhachis*, and merely indicated that it communicated between the 'temporal' (= trigemino/facialis) and 'supraotic' (= fossa Bridgei) chambers. Passive communica-

tion between the chambers seems to us to be an unlikely function of these foramina and, as discussed below, we suspect that they carried blood vessels.

In QMF21084, a groove runs forward down the medial wall of the trigemino/facialis chamber from the larger of the foramina that pierce the anterior wall of the fossa Bridgei; a comparable groove is seen in the skull of *Gogonasus* (ANU 49259), in which the foramen is single. Further, in ANU49259, a second groove runs forward from this foramen, along the mesial wall of the chamber, just beneath the dermal roof. In turn, this splits into two channels, one continuing further along the wall, and the other associated with a system of grooves on the undersurface of the supratemporal, adjacent to the spiracular notch. All this suggests that two structures passed through the anterior wall of the fossa Bridgei and ran forwards along the lateral wall of the braincase. The nature of these two structures is clarified by reference to features at the posteroventral edge of the fossa Bridgei in both *Cladarosymblema* and *Gogonasus*, as described below.

On the occiput of the *Gogonasus* skull (ANU49259), a groove enters the posterior edge of the fossa Bridgei from a ventromesial direction. From its position well posterior to both the foramen for nerves IX and X and the hyomandibular (see below), we believe that this groove carried a branch of the occipital artery, and not a dorsally coursing artery such as the orbital artery, which is normally in an anatomically more anterior position, and which always leaves the lateral aorta close to the hyoid arch (Goodrich, 1958: fig. 284). Once over the lip of the fossa Bridgei, the artery crossed the floor of the fossa, exiting anteriorly and giving rise to temporalis and supraorbital arteries of the trigemino/facialis chamber. A similar pattern can be seen in *Cladarosymblema* (Figs 29; 35), in some specimens of which the split evidently occurred before the passage through the anterior wall of the fossa Bridgei; in those specimens two foramina are seen here; in other specimens the split occurred after the wall was penetrated, and only one foramen is present. In QMF21084 a well-defined groove crosses the floor of the fossa and leads to the foramina. As noted above, specimens of *Cladarosymblema* show both patterns, which represent individual variation with no taxonomic significance.

This pattern of the occipital artery differs from that which Jarvik (1980: fig. 131) has shown in *Eusthenopteron*, in which the channels for the oc-

cipital artery are contained within the endocranial roof. As mentioned above, the space between the dermal roof and the endocranium in *Cladarosymblema* contains an anastomosing set of fine tubules (Fig. 31A,B) which we consider are connected with the vertically rising occipital artery. These tubules are much too fine to have carried the entire blood supply for the supraorbital, infraorbital and mandibularis arteries as shown by Jarvik (1980: fig. 131) for *Eusthenopteron*.

In *Cladarosymblema*, the crista parotica, which forms the outer wall of the fossa Bridgei and is best seen on QMF21085, is heavily ossified and firmly attached to the lateral edge of the tabular; it stands almost vertically. *Ectosteorhachis* (MCZ6499) is closely similar. About half of this vertical face on QMF21085 is occupied by a subcircular depression lined with vesicular bone that lacks a perichondral lining (Figs 32B; 33); this fossa received the dorsal head or process of the hyomandibular (see below). Immediately ventral to this surface, the bone on QMF21085 has been eroded away and reveals the jugular canal, which passes forward into the trigemino-facialis chamber. In QMF21085, the posteriormost parts of the canal begin to turn ventrally, an orientation matching that shown to better advantage on the more extensively preserved skull of *Gogonasmus* (ANU49259). The floor of the jugular canal in QMF21085 is penetrated by a large foramen, carrying the hyomandibularis branch of nerve VII (Figs. 32B; 33). The nerve ran dorsally and posterolaterally, in front of the auditory capsule in its passage from the cranial cavity, as in primitive gnathostomes generally (deBeer, 1937). It is likely as well that the orbital artery left the lateral aorta at this level and passed dorsally, as Romer (1937: 12; 1941: fig. 2) has supposed in *Ectosteorhachis*, but the ventral parts of the skull that would document its passage in *Cladarosymblema* are not preserved in the specimens that we have available.

Smithson & Thomson (1982), in their discussion of the hyomandibular in *Eusthenopteron*, hypothesized that the jugular canal carried the orbital artery through part of its anterior course, and such may well have been the case here. In fishes, the artery in the canal is well ventral to the floor of the fossa Bridgei, additional evidence that the orbital artery did not pass through the fossa. Furthermore, *Gogonasmus* shows a distinct notch on the ventral rim of the facet for the ventral hyomandibular process; perhaps this notch marks the ascent of the orbital artery, in which case the vessel passed anterior to the hyomandibular and

did not enter the jugular canal. Jarvik (1980: figs 78, 86) shows the orbital artery in a position anterior to the hyomandibular in *Eusthenopteron*, but passing through foramina that we believe were occupied by branches of nerve VII alone (see below). Below the jugular canal on QMF21085, the uppermost parts of the ventral articulation for the hyomandibular are lined with vesicular bone like that in the upper facet. Both facets are comparable in position to those in *Ectosteorhachis* (MCZ6499), but the canal in *Cladarosymblema* seems to have been substantially larger in diameter and located in a more ventral position. Given the limitations of the sample, the meaning of these differences is not known.

Ventral Surface. The ventral side of the endocranium of the otico-occipital unit is not well preserved in any of our specimens, but some useful information about its features is available. The notochordal chamber has robust walls, the internal surfaces of which show strong annular markings. Similar markings are seen in *Gogonasmus*, and presumably reflect the pattern of organization of the connective tissue sheath that surrounded the notochord. Enough of our material is preserved to show that a median space was originally present anteroventrally in the endocranium of the otico-occipital unit such that the walls of the notochordal canal did not meet to enclose the notochord anteroventrally (Figs 36B; 40). In life, an arcual plate presumably covered this space, as Jarvik (1980) has shown in *Eusthenopteron*. The more posterolateral region, around the vestibular fontanelle, is not preserved in any of our specimens. The skull of *Gogonasmus* shows that the bone is very thin here and, hence, would be easily destroyed, either prior to burial or in preparation. However, our comparative material of *Ectosteorhachis* (MCZ6499) shows no development of the vestibular fontanelle whatever; the area in this specimen is completely sheathed in bone, and the structure in *Cladarosymblema* may well have been the same. *Ectosteorhachis* shows no sign of a fenestra ovalis such as Jarvik (1980: 118, 126) has reconstructed as adjacent to the ventral surface of the articulation for the hyomandibular in *Eusthenopteron*.

A broad triangular surface of bone that served for the attachment of the basicranial muscles (Figs 36B; 40) forms the floor of the otic region. This continuous plate, which is best preserved in QMF21084, is composed of thick vesicular bone and is strongly attached to the equally thick walls

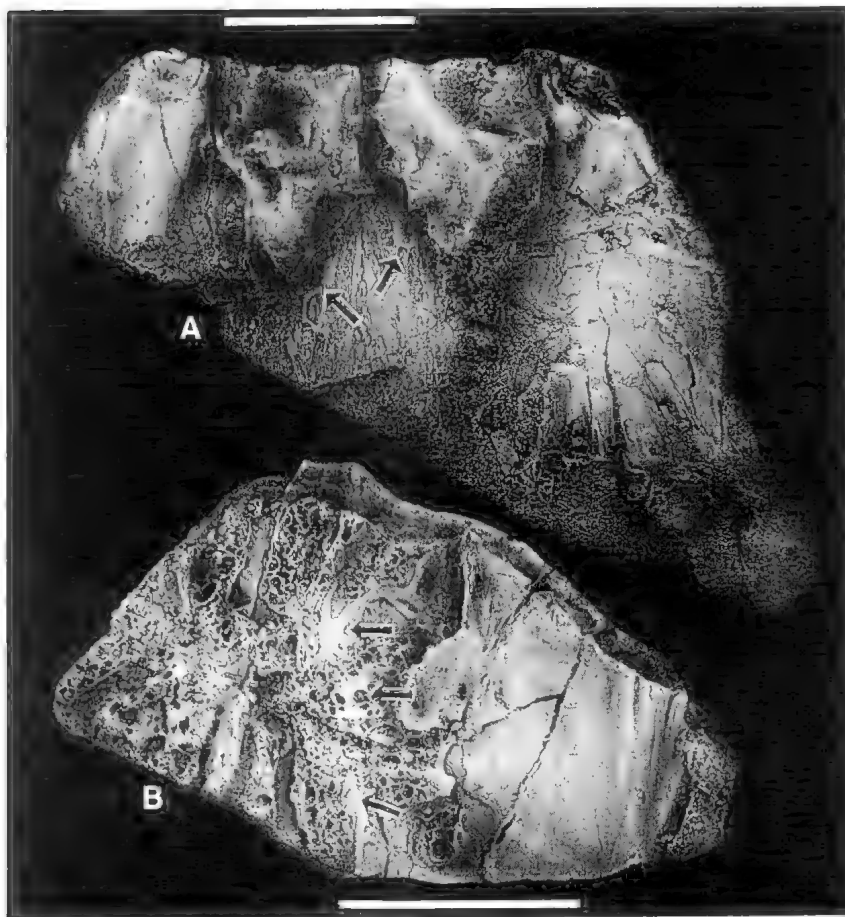


FIG. 31. *Cladarosymblema narrienense*. A,B, ventral views of incomplete otico-occipital shields, QMF26567 and 31863, with most of the endocranium removed to show reticulation of tubules between the roofing bones and the endocranium (arrows). Scale: 10mm.

of the notochordal chamber. Posterolaterally on this plate, a conspicuous foramen opening anteroventrally carried the palatal branch of nerve VII as it left the endocranium (Figs 36A,B; 37); a similar foramen occurs in *Ectosteorhachis* (MCZ6499) (see Romer, 1937: fig. 4) and is referred to by Jarvik (1980: fig. 78) as carrying the orbital artery as well as the nerve. Further anteriorly on QMF21085, and less well shown on QMF21084, on the dorsal side of the plate and lateral to the groove holding the jugular vein, a second foramen opens (Fig. 32B: white arrow); this foramen leads into a posteroventrally inclined tube which, although its posterior end is not exposed, seems to join with the canal for the hyomandibularis nerve. It must therefore be a branch of nerve VII. Romer (1937: fig. 2) labelled an opening in this position in *Ectosteorhachis* as

the hypotic branch of nerve VII. A foramen occurs in the same position in *Gogonasus* as well.

Perichondral Covering of the Braincase.

The posterior part of the braincase enclosing the brain stem is narrow, domed and with a floor that is distinctly arched from side to side. Posteriorly three to five foramina exit ventrolaterally on each side (Fig. 35). Presumably, these carried small vessels and spino-occipital nerves, including perhaps fibres of nerve XII. They undoubtedly connect with at least some of the several small foramina that open externally on the occiput on either side of the foramen magnum. Anteriorly, the roof of the braincase is composed of gently wrinkled perichondral bone forming a shallowly inclined surface that extends back posteriorly to the supra-otic cavity (Figs 32A; 36A,B; 37).

As QMF21085 shows,

at the level of this cavity the roof of the braincase rises abruptly and steeply, enclosing a deep pocket subdivided at the midline by a low ridge but no bony median septum. Although insufficient exposure of the region makes description difficult, it must have contained high pouches for the superior sinuses of the otic cavity and the endolymphatic sacs. Those of the two sides must have been in contact medially. Posteriorly from each of the pocket subdivisions, the foramen identified above as pertaining to the endolymphatic duct opens to the dorsal surface of the occipital shelf (Figs 38A,B; 39A,B). These spaces for the supra-otic cavities, the superior sinuses and the endolymphatic sacs, are very different in position and shape from those figured by Romer (1937) for *Ectosteorhachis nitidus*, and

we have no means of comparing them with *Megalichthys hibberti*.

Adjacent to the intracranial joint, the most anterior part of the roof of the braincase in the otico-occipital unit is marked by a distinct sub-circular depression, sometimes partly encircled by a horseshoe-shaped groove (Figs 32A; 36A; 37) (see QMF21084, 21085, 21109); two larger, shallower, and less distinct depressions are located posterolaterally to this. According to Jarvik (1980: fig. 89B) these depressions in *Eusthenopteron* probably reflect the position of the optic lobes in the roof of the brain. We see no reason to dispute this interpretation.

Three conspicuous foramina mark the passage of major nerves and a vein through the braincase wall into the trigemino/facialis chamber. Of the three, the anteriormost foramen is the largest and penetrates the wall more dorsally than the others (Figs 32B,C; 33; 41). It is the opening for the maxillary and mandibular branches of nerve V, corresponding in position to the same foramen in *Ectosteorhachis* (Romer, 1937: fig. 2; Thomson, 1967: figs. 1, 3). Immediately posterior to this, a second foramen opens at the end of an oblique tube that passes forward through the braincase wall. This foramen is well shown on QMF21085, and it carried the anterior lateralis branch of nerve VII in Romer's (1937) terminology, and the ophthalmicus superficialis ramus of VII in Thomson's terminology (1967); we prefer Thomson's terminology. Posteriorly from that point our specimens are damaged, and the surface where the oticus branch of nerve VII would be expected to have left the chamber wall has been impaired (Romer, 1937; Thomson, 1967). We have not been able to identify its foramen. Below and slightly posterior to the exterior ophthalmicus superficialis foramen, on QMF21085, a third, large foramen is present (Figs 32B,C; 33). Its ventral edge is not preserved in this specimen, but its dorsal rim is ventral to a thick horizontal ridge that in turn is ventral to the previously described nerve foramina. This opening marks the exit of the middle cerebral vein immediately prior to its junction with the jugular vein as the latter passed posteriorly in the jugular groove (see Romer, 1941: 153-154). The middle cerebral vein is a major drainage vessel of the endocranial cavity, and the size of this foramen in *Cladarosymblema* is in accord with its significance.

By contrast, in *Gogonasus*, there are only two major foramina anteriorly in the wall of the trigemino/facialis chamber, an anterior large one, for the mandibular and maxillary branches of

nerve V, and a smaller posterior one, for the anterior lateralis VII. Both are at the same level in the braincase wall, as in *Cladarosymblema*. Also as in *Cladarosymblema*, they are situated dorsal to a longitudinal ridge that extends along the inner wall of the braincase. The more extensive preservation of *Gogonasus* shows, however, that this ridge is simply the dorsal edge of a broad groove that ran along the internal surfaces of the cranial cavity near its floor. We suggest that this groove marks the limits of a lateral venous sinus, and that the middle cerebral vein drained from this sinus through the foramen in QMF21085, below the level of the foramina for the rami of nerve V and VII. In *Gogonasus*, however, there is no foramen here for the middle cerebral vein. Instead, there is a conspicuous notch lined with perichondral bone further forward at the anterior edge of the braincase wall; this notch also terminates the ventral groove. We suggest that these relations indicate that in *Gogonasus* the middle cerebral vein exited anteriorly, to join with the jugular vein within the soft tissues of the intracranial joint, anterior to its position in *Cladarosymblema*, *Ectosteorhachis* and, by implication, other megalichthyids.

Romer (1937) and Thomson (1967) indicated that the profundus branch of the trigeminus (nerve V₁) left the braincase in *E. nitidus* through soft tissue between the two units, and we have no evidence to indicate that the nerve followed a different course in *Cladarosymblema*. Dorsal to the level of the nerve foramina, the braincase wall of QMF21085 is marked by a series of parallel, irregularly vertical ridges (Fig. 32C). These probably reflect the attachment of palatal levator muscles.

In *Eusthenopteron*, Jarvik (1980) has identified a depression on the posterior wall of the trigemino/facialis chamber, adjacent to the spiracular notch in the dermal roofing bones, as indicating the position of the spiracular diverticulum; Thomson (1967: fig. 1) shows the spiracular diverticulum in the same position in *Ectosteorhachis*. One of our specimens of *Cladarosymblema*, QMF21085, has a shallow depression here bordered by two pairs of blunt, knob-like processes, one above the depression, the other below; none of our other specimens is preserved in this region. In *Gogonasus*, a shallow depression occurs in a somewhat more mesial position on the posterior wall of the chamber, beneath the foramen for the occipital artery or its branches. In keeping with Jarvik (1980) and Thomson (1965, 1967), we suggest that this depression marks the position of the spiracular di-



FIG. 32. *Cladarosymblema narrienense*. A-C, anteroventral, and right and left lateral views of incomplete otico-occipital unit, QMF21085. In A, white arrows indicate foramina for the occipital artery in the anterior wall of the fossa Bridgei. In B, black arrows indicate the dorsal and upper part of the ventral hyomandibular attachments. White arrow indicates position of hypotic branch of nerve VII as it exits the endocranium. Parts of both the left and right walls of the braincase have been broken away so that the foramina on the left side of the braincase are more clearly exposed than those on the right. The photographs have been made to show these to advantage. Asterisks indicate positions of nerves and vessels on the left side of the braincase, viewed from inside the braincase in B and from outside in C. (See Fig. 33 for interpretation.) Scales: 10mm.

verticulum in both *Cladarosymblema* and *Gogonasus*.

In our specimens of *Cladarosymblema*, the saccular region of the otic capsule is not well preserved and we are unable to determine the

configuration of the sacculus, utriculus and the relevant nerves. However, in QMF21084 it is possible to infer that the sacculus is not as extensive laterally as the sacculus illustrated by Romer (1937: figs 8,9) for *Ectosteorhachis*, because it has to fit within the confines of the surrounding bones. Only a fragment of the utriculus is represented on the same specimen, and it must have been only a slight swelling. The horizontal and posterior vertical semicircular canals are best shown on QMF21085 (Fig. 34A), but they cannot be seen in their entirety. The vertical canal must have been more depressed than semicircular to fit beneath the roofing bones.

HYOID SERIES

Hyomandibular. One well-preserved right hyomandibular, QMF21107, is known from *Cladarosymblema*. It resembles that of *Eusthenopteron* in general but differs significantly from all available descriptions and figures of that element in several ways. Among the more important of these is its display of features that Jarvik (1954) described for the *Eusthenopteron* hyomandibular, but which Smithson & Thomson (1982) had not found during their more recent review. Despite its importance for the study of the origin of tetrapods, the bone is poorly known in osteolepiforms, with extensive descriptions only for *Eusthenopteron* and *Ectosteorhachis* (Eaton, 1939; Romer, 1941; Westoll, 1943).

The hyomandibular of *Cladarosymblema* is deeper relative to its length than that of *Eusthenopteron* (compare our Figs 43 & 44 with Jarvik, 1980: fig. 107) but, as in the older genus, it is narrow mesiolaterally; that of *Ectosteorhachis* is more rod-like. Although relatively large when compared with the tetrapod stapes, the hyomandibular appears to have been constructed of delicate vesicular bone covered by a thin, dense layer of perichondral bone on all its external surfaces except the anteroventral extremity. This light construction of the hyomandibular contrasts with the much denser bone of the lateral walls of the braincase in the area of articulation of the hyomandibular to the side of the skull. In that sense, the hyomandibular of *Cladarosymblema* is not a massive bone at all (see Romer, 1941: 150).

At its proximal end, QMF21107 shows two vertically ovoid facets of unfinished bone, the dorsal and ventral processes; the dorsal process is slightly deeper and anteroposteriorly narrower than the ventral process. Between the two processes is a thin lamina of perichondral bone (Fig.

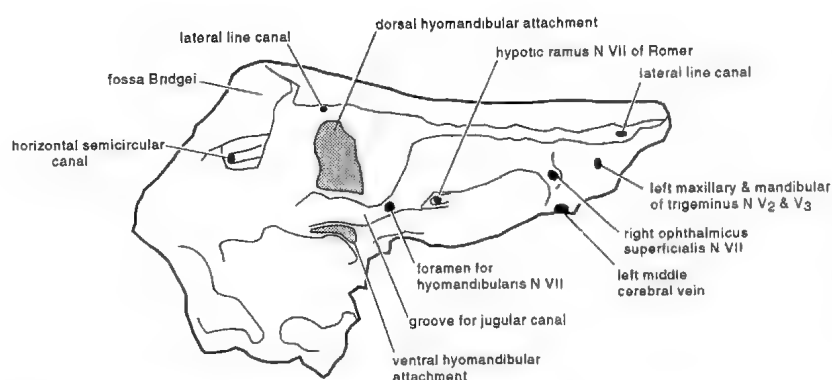


FIG. 33. Outline drawing of the view shown in Fig. 32B.

43H), much as described by Romer (1941) for *Ectosteorhachis*, and Smithson & Thomson (1982) for *Eusthenopteron*.

Only one specimen in our collection, QMF 21085, clearly preserves the articulating surfaces of the skull that supported the hyomandibular (Fig. 32B; 33). The large dorsal facet lies on the lateral wall of the fossa Bridgei and extends from just beneath the skull roof to the dorsal margin of the jugular canal. The lower facet borders the jugular canal ventrally, but only the dorsalmost extent of this facet is preserved on our specimen. Nonetheless, it is evident from QMF21085 that in *Cladarosymblema* much of the jugular canal between these facets was open laterally, with the lateral commissure being limited to a more anterior position. In this respect, *Cladarosymblema* closely resembles both *Ectosteorhachis* (MCZ6499) and *Gogonasmus* (ANU49259), in which the lateral commissure is limited to a thin strip of bone entirely anterior to the hyomandibular; in both these genera also, the jugular canal is open laterally at the level of the hyomandibular.

The dorsal margin of the hyomandibular of *Cladarosymblema* continues distally in a nearly horizontal direction for slightly more than half of the total length of the bone (Figs 43E,G; 44A,C). This margin is crossed by a well-developed dorsal groove that obliquely traverses the hyomandibular, and then continues down on to its anterolateral side (Figs 43E,F; 44A-C). The perichondral bone that lines this groove is more dense than that of the adjacent surfaces, which appear somewhat spalled on this specimen, and this feature, combined with the geometry of the groove itself, can leave no doubt that this structure was real, and that it has anatomical significance. As final confirmation, the groove has its obvious counterpart in *Gogonasmus* (Fig. 45A,B,E), where it has the

same orientation as in *Cladarosymblema*.

Jarvik (1954) described a groove comparable with this in the hyomandibular of *Eusthenopteron*; he believed the groove carried the ramus hyoideus of the hyomandibular trunk of nerve VII. In the *Eusthenopteron*

hyomandibulars available to them, however, Smithson & Thomson (1982) found the dorsal

groove to be variable in its occurrence, not recognized at all on one individual (the 'Gosselin' skull), but 'reasonably distinct' on the right side of ROM1234, a braincase with associated hyomandibulars. Smithson & Thomson (1982) concluded that the groove Jarvik had described was of no significance. They argued that its more medial parts were an artifact of preservation, the lateral parts were variable in occurrence (as already noted), and that in no living fishes does the hyoid ramus loop dorsally over the hyomandibular. However, our specimens indicate that Jarvik was correct, at least in his determination that the dorsal groove is an anatomically real feature of the hyomandibular in osteolepiforms. Indeed, the hyomandibular of *Gogonasmus* shows that not only is the dorsal groove present, but that it continues down on to the anterolateral face of the bone, towards a conspicuous depression (see below) adjacent to the distal opening of the hyomandibular canal (Fig. 45A,B). We have observed that in other parts of the cranial skeleton of *Cladarosymblema*, impressions of nerves and vessels into bone surfaces are highly variable between individuals; we therefore do not accept that the absence of a groove in some specimens of *Eusthenopteron* is valid evidence that no structure crossed the hyomandibular dorsally. The presence of this groove in specimens representing three divergent osteolepiforms, *Eusthenopteron*, *Cladarosymblema* and *Gogonasmus*, indicates that it was a feature of primitive osteolepiforms.

But what did it carry? If Jarvik's (1980) argument that it carried the hyoid nerve is to be accepted, one must confront the objection by Smith & Thomson that no modern fish species shows a similar course for this nerve. Alternatively, the groove may have carried a vessel, but

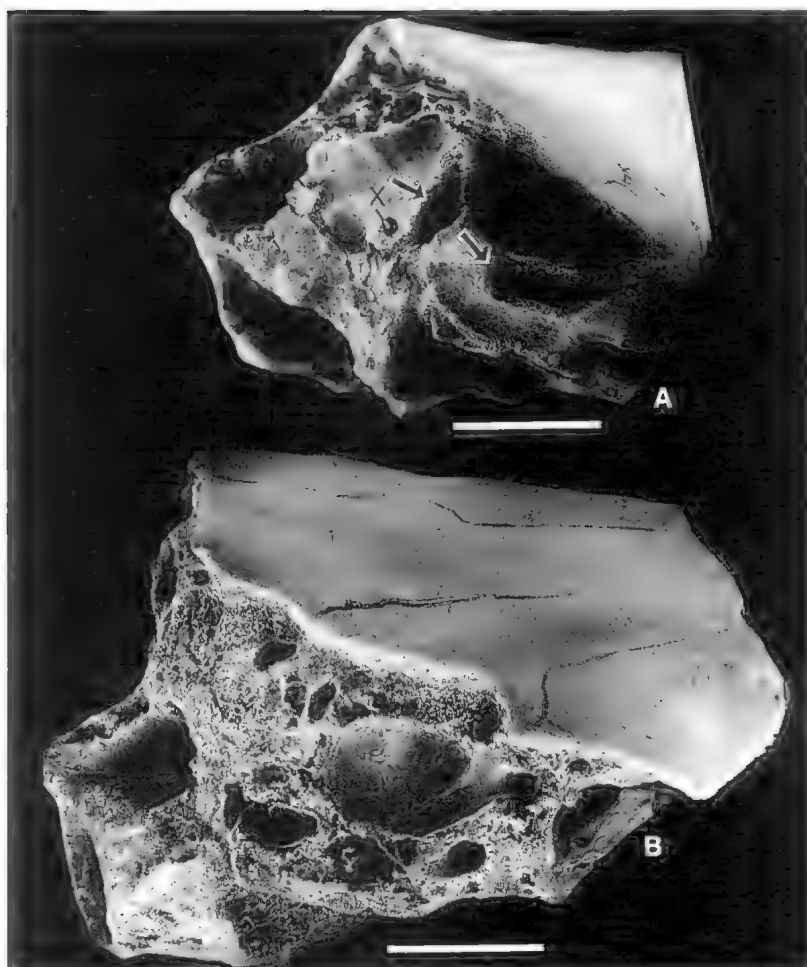


FIG. 34. *Cladarosymblema narrienense*. A, posterolateral view of an otico-occipital unit showing the wall of the endocranium, QMF21085; arrows indicate vertical and horizontal semicircular canals, and X indicates the foramen for the posterior lateral line nerve. (See also Fig. 35.) B, lateral and slightly posterior view of QMF21084, which has an eroded posterolateral wall of the endocranium exposing several otherwise unknown features. For explanation see Fig. 35. Scale: 10mm.

similar impediments apply to this interpretation. The only vessel that suggests itself as relevant is the efferent hyoid artery. In *Eusthenopteron*, according to Jarvik (1980: fig. 107), this artery entered the hyomandibular accompanying the hyomandibular nerve. But if it followed the dorsal groove, the artery arose in a mesial position at its proximal extremity (behind the hyomandibular) coursing to a lateral position distally, in front of the hyomandibular. The skull of *Gogonasus* (see ANU49259; WAM86.9.661) provides additional evidence bearing on this problem. Especially well defined on the right side, is a short,

shallow groove that leaves the posterior opening of the jugular canal dorsally and curves towards the dorsal facet of the hyomandibular. When the hyomandibular is manually articulated to the skull in this specimen, the most proximal part of the hyomandibular groove is brought immediately adjacent to the groove from the jugular canal. Clearly, the two grooves reflect the course of the same structure, either a vessel or a nerve; the available evidence is inadequate to determine which.

Along the dorsal edge of QMF21107, distal to the dorsal groove, is a depression exposing vesicular bone (Figs 43E,F; 44A,B); in life this was probably continued dorsally in cartilage. A low bony process arises in this same position on the hyomandibular of *Gogonasus*, and partially borders the dorsal groove mesially. Beyond this depression in *Cladarosymblema*, the dorsal margin of the hyomandibular abruptly descends obliquely to the most distal extremity of the bone as in *Ectosteorhachis* (Romer, 1941: fig. 1). The dorsal margin is not smoothly curved as is

shown in Smithson & Thomson's (1982) figure of the *Eusthenopteron* hyomandibular. In *Gogonasus*, the descent of the dorsal margin distally is also abrupt, but not at as steep an angle as in *Cladarosymblema*. The most proximal parts of the descending dorsal edge on QMF21107 are widened and enclose an elongate depression of vesicular bone that lacks a perichondral covering. Here, too, this area in life must have been capped or otherwise continued in cartilage. A comparable surface is seen on the hyomandibular of *Gogonasus* (Fig. 45). This depression clearly corresponds to what Romer (1941) has identified

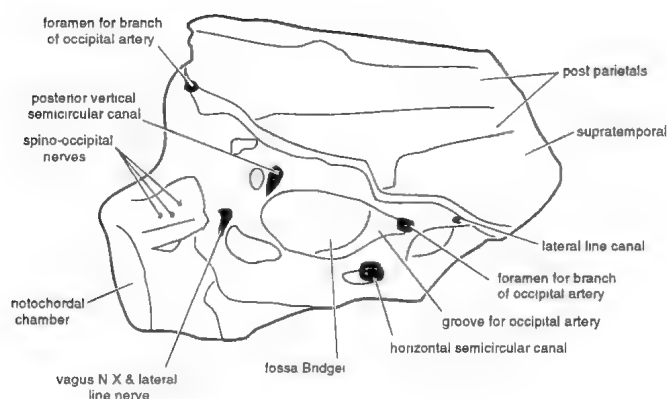


FIG. 35. Key to Fig. 34B.

as the opercular process in the hyomandibular of *Ectosteorhachis*, and Jarvik (1954) in *Eusthenopteron*. However, Smithson & Thomson, together with Westoll (1943), saw no process or other structure in that position. Its presence in *Cladarosymblema*, *Gogonasmus*, and at least some individuals of *Eusthenopteron* (its apparent absence from other individuals may well be an artifact of preservation) implies that a connection between the hyomandibular and opercular is primitive in osteolepiforms. Indeed, the internal surface of the opercular of *Cladarosymblema* appears to have an attachment surface in this position (see below). This is not surprising in view of the accounts of primitive fishes by Lauder (1980a,b;1985).

Smithson & Thomson (1982) identified a preopercular process on the lateral side of the hyomandibular of *Eusthenopteron*, beneath the distal opening to the hyomandibular canal. Neither *Cladarosymblema* nor *Gogonasmus* shows a process, tuberosity, or any other discontinuity of the surface here that might indicate an articulation between the hyomandibular and preopercular. In any case, an attachment between the preopercular and hyomandibular is unexpected on functional grounds. The preopercular is normally a fixed bone, whereas the hyomandibular is an integral component in the kinetic action of the skull, as Thomson (1967) has already shown.

Overall, the anterolateral side of the hyomandibular in *Cladarosymblema* is dorso-ventrally convex. However, as mentioned above, it is marked distally by the deep depression that is adjacent to the lower opening of the hyomandibular canal. Similar features are present in the hyomandibular of *Gogonasmus*. The

hyomandibular canal opens proximally on the posteromesial side, which is concave, at the end of a short deep groove that begins between the dorsal and ventral processes. When the hyomandibular is manually articulated with the skull in both *Cladarosymblema* and *Gogonasmus*, this groove, and hence the hyomandibular canal, is in open continuity with the jugular canal passing mesially to it, with the lateral commissure occupying a more anterior position. This means that there is no bony separation between the two canals, and the hyomandibular nerve could turn directly into the canal at the

base of the hyomandibular. Whereas the posterior opening of the jugular canal appears to occupy this same relationship to the hyomandibular in *Eusthenopteron*, the lateral commissure extends further anteriorly and the fully enclosed parts of the canal are comparatively longer than in either *Cladarosymblema* or *Gogonasmus*. All authors appear to agree that the hyomandibular canal carried the rami mandibularis externus and internus (chorda tympani), and we see no reason to conclude otherwise for *Cladarosymblema*.

The posteromesial surface of QMF21107 shows other features of interest, and at least some of these also occur in *Gogonasmus*. Distal to the proximal opening of the hyomandibular canal on QMF21107, the more dorsal parts of the posteromesial face are occupied by an elongate depression having a well-defined ventral rim and a surface crossed by several short, irregular ridges (Figs 43G; 44C). A similar depression is seen in *Gogonasmus*. This depression probably furnished the attachment area for the adductor hyomandibularis muscle, with its most ventral extent marked by the ventral rim. Romer (1941: fig. 1) believed that this groove in *Ectosteorhachis* marked the course of the vena capitis lateralis (=jugular vein), but manual articulation of the hyomandibular on the skull of *Gogonasmus* shows that the jugular canal is too mesial and curves in too marked a ventral direction opposite the hyomandibular for the groove to reflect the passage of the vein. Also occurring within the adductor depression, but well set off distally from the opening of the hyomandibular canal, is a short oblique groove that leads to a narrow canal. From the angle of the orientation of this groove, the canal probably merged with the hyomandibular



FIG. 36. *Cladarosymblema narrienense*. A-B, anterior and ventral views of QMF21084. Note particularly the foramina for the lateral line canals lateral to the articular processes in A (arrows), and the foramina for the palatal branch of nerve VII (arrows) in the flat triangular plate for the attachment of the basicranial muscles, in B. For interpretation see Fig. 37. Scale: 10mm.

canal within the hyomandibular; there is no alternative exit visible externally. The left hyomandibular of *Gogonasmus* shows what is undoubtedly the homologous foramen, but in that specimen it is located closely adjacent to the proximal entrance of the hyomandibular canal, being separated from it by only a narrow bridge of bone; this bridge has been broken away on the right hyomandibular of the same specimen. Jarvik (1954) and Smithson & Thomson (1982) illustrated a foramen in this position in *Eusthenopteron*; Jarvik (1954) identified it as a foramen for a vein, and Smithson & Thomson (1982) left it unidentified. Its undoubted occurrence in *Eusthenopteron*, *Cladarosymblema* and

Gogonasmus indicates that it is a real feature, a conclusion supported by the groove associated with it in QMF21107. Perhaps as Jarvik (1954) suggested, it carried a vein; but to us it seems more probable that it carried a nerve which, from its position on the mesial side of the hyomandibular, would have been the opercularis ramus of nerve VII. In *Ectosteorhachis*, Romer (1941: fig. 1) illustrated a foramen for the opercularis nerve distally on the side of the hyomandibular; there is no foramen in this position on QMF21107.

On QMF21107 beneath the ridge marking the ventral limit of the adductor hyomandibularis musculature is a long narrow groove that extends from the ventral process to the lateral edge of the bone, beneath the opercular process (Figs 43G; 44C). Romer (1941) identified a groove in this position in *Ectosteorhachis* as indicating the path of the pretrematic branch of the glossopharyngeal (IX) nerve. Smithson & Thomson (1982) reported that this groove is absent in *Eusthenopteron*. It is present and well defined in both *Cladarosymblema* and *Gogonasmus*, although it is very nearly straight in *Gogonasmus*. No other conspicuous features are present on the mesial face of the hyomandibular in either *Cladarosymblema* or *Gogonasmus*.

Smithson & Thomson (1982) identified a distal surface that could mark the attachment of the stylohyal, but neither QMF21107 nor the *Gogonasmus* hyomandibulars are well enough preserved in this area to provide any additional information that might confirm this articulation or allow further elaboration of its features.

In the osteolepiform hyomandibular, the hyomandibular canal crosses from its mesial, proximal entrance to a lateral and distal exit, opening in a deep depression (see above) towards the distal end of the bone. Along the dorsal side of this depression in *Cladarosymblema* (Fig. 43E) is a system of short irregular ridges and pits that served as attachment surfaces for the protractor hyomandibularis muscle (Jarvik, 1954; Smithson & Thomson, 1982). In *Gogonasmus*, this depression is shallower on the right hyomandibular than on the left, but on both there is a well-developed complex of irregular surfaces consistent with muscle attachment (Fig. 45A,F). The right hyomandibular of the *Gogonasmus* specimen has particularly well-preserved surfaces in this area. The specimen clearly shows the dorsal groove continuing down the lateral face of the bone into the distal depression, running proximally and ventrally to the scars for the protractor muscle.

The hyomandibular canal carried the hyomandibular nerve; whether it was divided into external and internal mandibular rami within the canal or only after exiting the canal, is not known. On QMF21107 the canal has been cleared of matrix; direct inspection of its walls gives no indication of a subdivision such as would be expected if the canal carried two major nerve rami within it. More distally, but still within the confines of the hyomandibular, it appears that the nerve split, following the pattern seen in other osteolepiforms: the more dorsal trunk, presumably the ramus internus, left by passing under a small bridge of bone, incomplete on our specimen; the other, the ramus externus, passed over a raised platform or pad of bone distally on the hyomandibular before continuing onward to the lower jaw (Fig. 43E). These features are not preserved on the *Gogonasus* specimens; Smithson & Thomson (1982) report a distal bridge of bone in the same position as that on QMF21107, but it is complete.

Urohyal*. Laterally compressed bones (QMF26573, 26574 and 26576) that have a short anterior stem and a blade-like posterior section, represent the urohyal of this species (Fig. 43A-D). In making this interpretation we have taken into account that these bones are obviously from the midline of the animal; they are cartilage bones with a thin perichondral layer on the lateral, ventral and dorsal surfaces, and exposed dense endochondral bone at the anterior and posterior ends; the bone texture is very similar to that of a large number of visceral bones found in the same etches; and the bones have a shape similar to that of the urohyal in *Eusthenopteron foordi* (Jarvik, 1980: fig. 112D). The anterior stalk is about half the length of the bone, is elliptical in cross-section with the long axis of the ellipse vertical. The posterior blade is approximately two-thirds as high as long, has a truncated posterior end and a variably shaped anterior end. The posterior edge is truncated, and low on its surface an isthmus of perichondral bone separates a large dorsal and a smaller ventral surface to which other cartilagenous elements were attached. Its posterior end is less angular than that of the urohyal of *E. foordi*. Both the ventral and dorsal surfaces of the blade are distinctly flattened. Jarvik (1980: vol.2, figs 109; 117) showed the geniohyoideus and hyogenioglossus muscles attached to the blade of the urohyal in *Eusthenopteron*. The blade in *C. narrienense* shows strong concentric ridges that we interpret as reflecting growth stages; they are not interrupted as would be expected if muscles

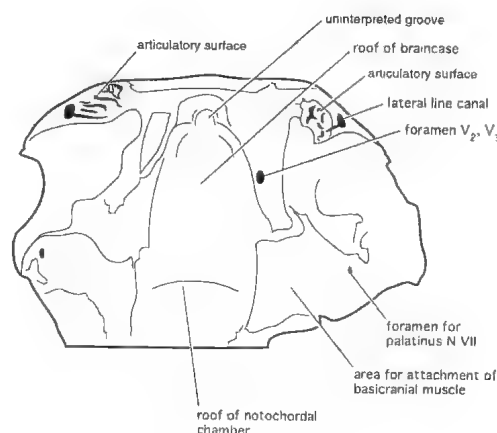


FIG. 37. Labelled key to Fig. 36A.

were attached to these surfaces. So far as we are aware, no other megalichthyid urohyal is known.

MANDIBLE

We have more than 20 mandibular elements, some preserved as more or less complete rami, but the majority fragmentary (Figs 46-51; 54-56; 57A-G). Nine specimens have the posterior end at least partly preserved, and of these eight provide significant information on the glenoid fossae and the foramina and grooves in the vicinity of the articulation. The smallest complete specimen is only about half the size of the largest. The fractured specimens are very valuable because they provide information on the lateral line canals and the grooves in the open spaces within the jaw. One specimen, QMF31861, consists of the external dermal bones from the posterior extremity with part of the articular still attached, and a second one, QMF21100, has the same posterior part preserved and extends a little further anteriorly. These specimens have been particularly useful because they exhibit the courses of the canals from the exterior into the Meckelian space as well as the lateral line entry point. This wealth of material provides the opportunity for a discussion of variation that is unusual for the osteolepiforms.

General Form. In lateral profile (Figs 46A; 48; 49A,D) the mandible varies in height systematically along its length, the minimum height / maximum height ratio being c.0.75. Posteriorly the dorsal edge turns downwards as it does in *Megalichthys*, but unlike some specimens of that genus, the ventral edge invariably turns upwards towards the posterior end of the mandible. The maximum mandibular height is a short distance

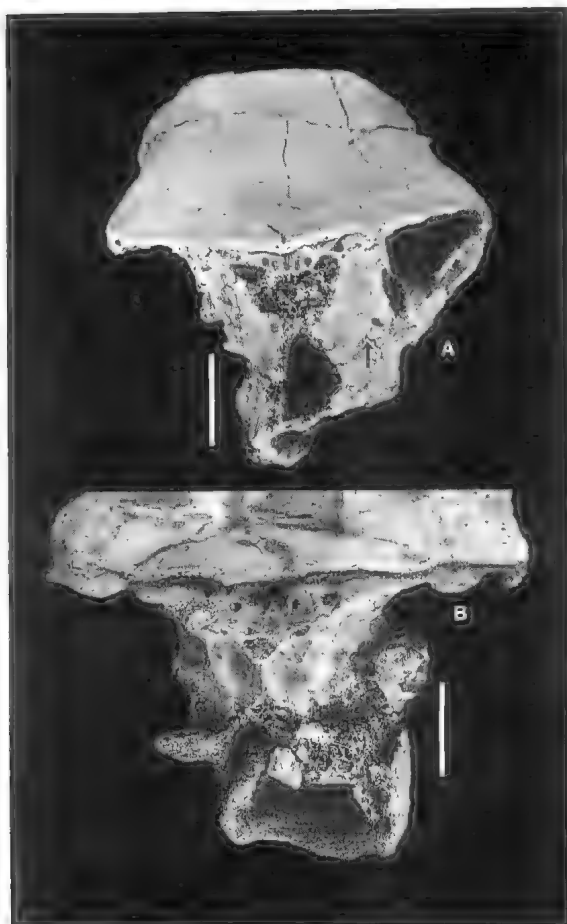


FIG. 38. *Cladarosymblema narrienense*. A, B, posterodorsal views of two otico-occipital units, QMF21084 and 21094. The vagus nerve X foramen, indicated by an arrow, is hidden beneath a ledge of bone. (For lateral view of A see Fig. 34A, and for its interpretation, Fig. 39.) Scale: 10mm.

in front of the glenoid articulation and not near the anterior end of the jaw (cf. the mandible of *Gogonasus* in Fig. 52A,B). Towards the anterior end, most individuals show an embayment in the ventral edge, its depth varying from specimen to specimen. Presumably it allowed for the articulation of some of the submandibulars, but, as is shown below, it also made space for the passage of a nerve and an artery. In dorsal view, the curvature shows an increase anteriorly (Figs 46C; 47B; 49C).

A submandibular furrow of variable depth lies along the ventral edge of the mandible just inside the external dermal bones. This furrow has two distinct parts, an outer surface on the infradentaries for the articulation of the submandibulars, and

an inner deeply concave surface along which traversed nerves and vessels which are discussed below. The double nature of this furrow is well shown in Figs 46D and 49E.

External Dermal Bones. The external dermal bones are all cosmine-covered and are usually smooth. However, two individuals, QMF21101 and 21090 (Fig. 49A,D, respectively), display areas of resorption. In the former, patches where the cosmine has been removed are obvious; the latter has less continuous areas of resorption, and some of these contain irregular blisters of new cosmine that rise above the general surface. These blisters resemble some of the new-growth cosmine on the scales, the significance of which will be discussed below when dealing with scale morphology.

The sutures between the external dermal bones cannot be recognised consistently on any specimens, irrespective of their size, thereby creating a major problem for us when comparing *Cladarosymblema* with other species. On most specimens, a clear incision is observed approximately in the position one would expect to find the suture that separates the dentary from the infradentaries, but it becomes obscure anteriorly. Within this incision a row of pores of the same kind as those that occur in other pit-lines can be seen, so there is no question that the incision is a pit-line and not a suture. This is in accord with previous work (Watson, 1926; Jarvik, 1942, 1980; Borgen, MS), but the pit-line has been considered by most workers to lie along the suture between the dentary and the infradentaries. However, X-radiographs of three specimens from which the internal bones have been removed, show that most of the ventral edge of the dentary lies dorsal to the pit line and diverges from it (Figs 54-56). Jarvik (1980) recorded that the dentary in *Eusthenopteron* is overlapped by the infradentaries, and it is clear that such an arrangement could cause difficulty in the interpretation of X-radiographs. Broken edges of mandibles of *C. narrienense*, however, show no sign of such an overlap. This implies that the standard interpretation of *Megalichthys* (Watson, 1926; Borgen, MS) needs to be re-examined, a process that can be undertaken only by sectioning or X-radiography.

The sutures between the infradentaries are not obvious on the external surface of any of our specimens, but two, QMF21088 and 21030, show rows of peculiar short oblique *en echelon* markings in the approximate position of the angular/surangular and the postsplenial/angular

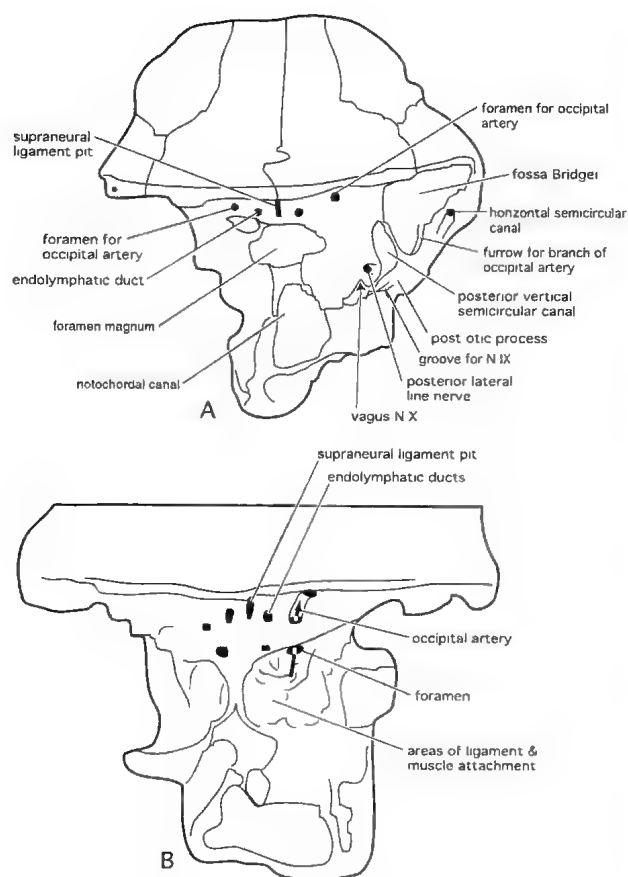


FIG. 39. Labelled key to Fig. 38.

sutures; a third, QMF31867, has what are probably incomplete surangular/angular and angular/postsplenial sutures (Fig. 55A: arrows). The interpretation of these markings is not clear, although on one specimen, QMF21089, they have been observed in line with a definite suture, and might therefore be thought to mark an extension of a suture. However, such a view is untenable, because such markings have also been found on a lateral gular (QMF26543) where they are obviously not related to sutures. X-radiographs show the centres of ossification of the infradentaries, and these can be confirmed on the internal surfaces of some bones; the boundaries between these bones can be defined with some confidence by the joint use of X-rays and radial markings around the centres of ossification on the bone interiors. The very posterior position of the centre of ossification of the surangular is a remarkable

feature, as is the great size of that bone. Note that we have been unable to find the boundary between the splenial and postsplenial. This does not mean that we consider the two bones to be fused, but rather that the suture cannot be seen on any of our material. The most probable reconstruction of the external dermal bones is given in Fig. 48.

The horizontal pit-line is well developed on all specimens. It rises to, or almost to, the dorsal edge of the mandible just posterior to its highest point. From there it turns posteroventrally parallel with the edge of the cosmine, although it shows some minor flexing in some specimens. This line isolates a cosmine-covered strip from which a low naked blade rises up against the anterolateral wall of the articular (Figs 46A; 49A,D). In *M. hibberti*, Watson (1926: fig. 37) and Borgen (MS) record marked deflections of the horizontal pit-line where it meets the sutures between the infradentaries. No such deflections are present in *C. narrienense*, in which the line is straight or only gently flexed.

A vertical pit-line is situated towards the front of the mandible, approximately in the same vertical plane as the anterior coronoid tusk. It is never straight, but stands vertical in its lower course from the ventral edge, bending

forwards to a variable extent towards its upper edge in different specimens (Figs 46A; 48; 49D). The extent of the bending is not correlated with the size of the specimen. On several specimens a group of special sensory pores lies either slightly in front of the vertical pit-line or straddling it. Where this group has not been observed, its absence is probably the result of cracking or abrasion.

Small teeth occur along the dentary from a point just behind the anterior end of the adductor fossa almost to the median symphysis. The crest of the dentary is formed of finished bone with the cosmine turned inwards slightly, and the teeth stand inside this edge at a somewhat lower level. The teeth vary little in size, are turned slightly inwards, and are too poorly preserved to determine their replacement pattern. Inside the tooth row along most of its length, there is only a very narrow shelf against the coronoids. Lateral to the median symphysis, however, the dentary thick-

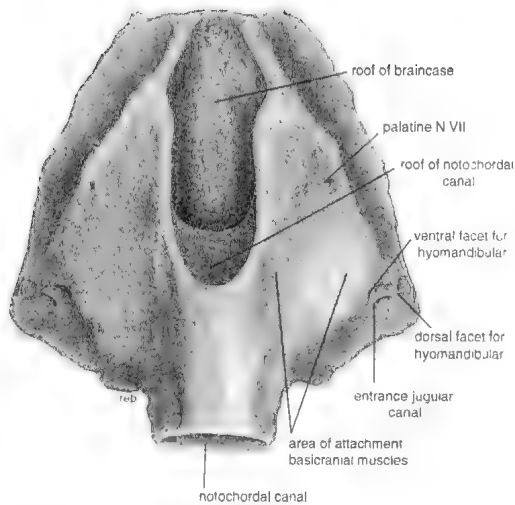


FIG. 40. *Cladarosymblema narrienense*. Reconstruction of the otico-occipital unit in ventral view, based on all available specimens.

ens and widens to form a wider shelf, which carries a tusk and one or two pits (Figs 46C; 47B; 50D,E; 57A-E). As the dentary shelf widens, it carries a distinct groove that continues around the front of the jaw anterior to the parasymphysial plate. The row of small teeth that runs along the dentary is usually absent in front of the tusks, but occasionally the teeth in the row are only reduced in number (Fig. 57A,B,D).

The tusks are strongly folded at their bases, and their replacement pits have radially arranged ridges of bone of attachment. The small marginal

teeth also have folded bases, but the folding is weak. Details of the teeth and tusks are given below.

The lateral line canal enters the mandible posterolaterally to the glenoid fossa, and at first runs anteroventrally. As it approaches the edge of the specimen, near the ossification centre of the angular, it turns through a gentle arc to run parallel with the ventral edge of that bone, from which it is separated by about 2-3 mm. The canal is deeply buried over its entire length. It opens to the exterior via a number of large pores that are scattered on either side of its course, but which occasionally form a single line. As shown on Figs 55C and 56, the arrangement of a second row of pores below the main canal is served by a more-or-less regular set of tubules. The canal and its pores are deflected around the embayment in the ventral edge previously mentioned. Anteriorly the canal joins its fellow below the large symphysial area of vesicular bone. There is no oral branch of the canal in the surangular, and no sign of a pit-line on that bone. Owing to inadequacy of description and illustration, it is difficult to determine from the literature if this is an unusual feature in osteolepiforms.

The external dermal bones at the median symphysis are not complete, a space being left for a small bone between the ventral edges of the splenials, as in *Megalichthys hibberti*. This bone is always missing on our specimens, indicating that it was not fused into the dermal series. Such a feature is present also on *M. hibberti* (Watson, 1926; Borgen, MS), and we consider that it is a family character.

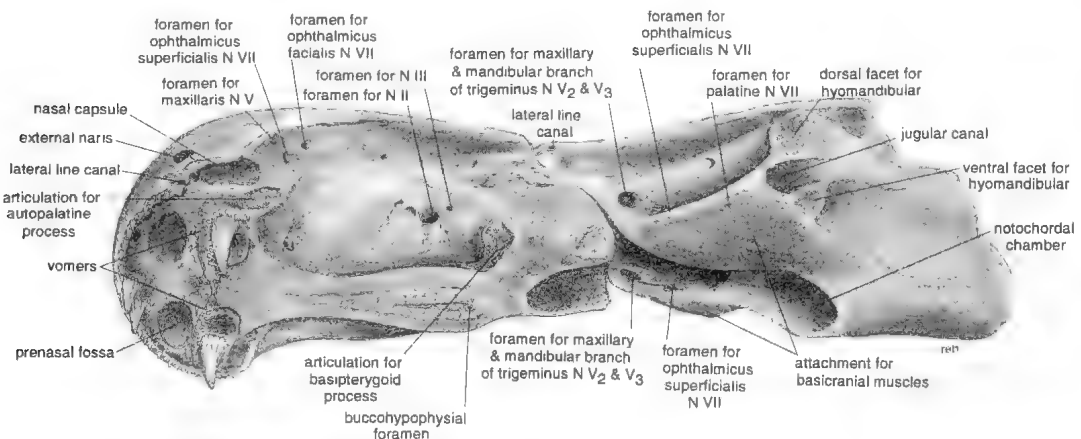


FIG. 41. *Cladarosymblema narrienense*. Labelled reconstruction of the assembled units of the cranium, showing the main features of the skeleton.



FIG. 42. *Ectosteorhachis nitidus* Cope. A,B, posterior and ventral views of MCZ6499, to show the depressed nature of the roof and the fossa Bridgei. C, ventral view of MCZ6999, part of a cranium showing the small submandibulars and the large median gular with lyre-shaped pit-lines particularly well. The right principal gular shows a very transverse anterior edge and a longitudinal crack. The apparent suture on its right side has not been identified. Scale: 10mm.

Articular and Meckelian Bones. The articular bone is thick and long, forming a sloping posterior surface to the adductor fossa (Figs 46C; 47B; 49C,F). This surface always carries ridges that presumably indicate the positions of attachment of the adductor muscles. The doubled glenoid fossa is hourglass-shaped, the two fossae being in contact (Figs 46B,C; 47B; 49C; 50B; 57F). They are floored by coarse vesicular bone, and must

have been invested with moderately thick cartilage in life. The transverse axis of the whole structure is not set at right angles to the sagittal line; the inner fossa is slightly anteromesial and ventral to the lateral fossa. The significance of this arrangement is discussed in the section on Functional Interpretation below. Ventrally, the articular is exposed between the surangular and the prearticular, its extent being well displayed on



FIG. 43. *Cladarosymblema narrienense*. A,B, left and right lateral views of urohyal, QMF26574. C,D, right and left lateral views of another urohyal, QMF26573. E, anterolateral. F, dorsal. G, posteromesial. H, anterior and slightly lateral views of right hyomandibular, QMF21107. Scale: 10mm.

QMF21088, 21000 and 21102 (Figs. 46D; 50C). It occupies most of the posteroventral surface of the mandible, and diminishes in width anteriorly,

where it forms the inner wall of the submandibular furrow. Approaching the symphyseal region it becomes more extensive (see below). The extent

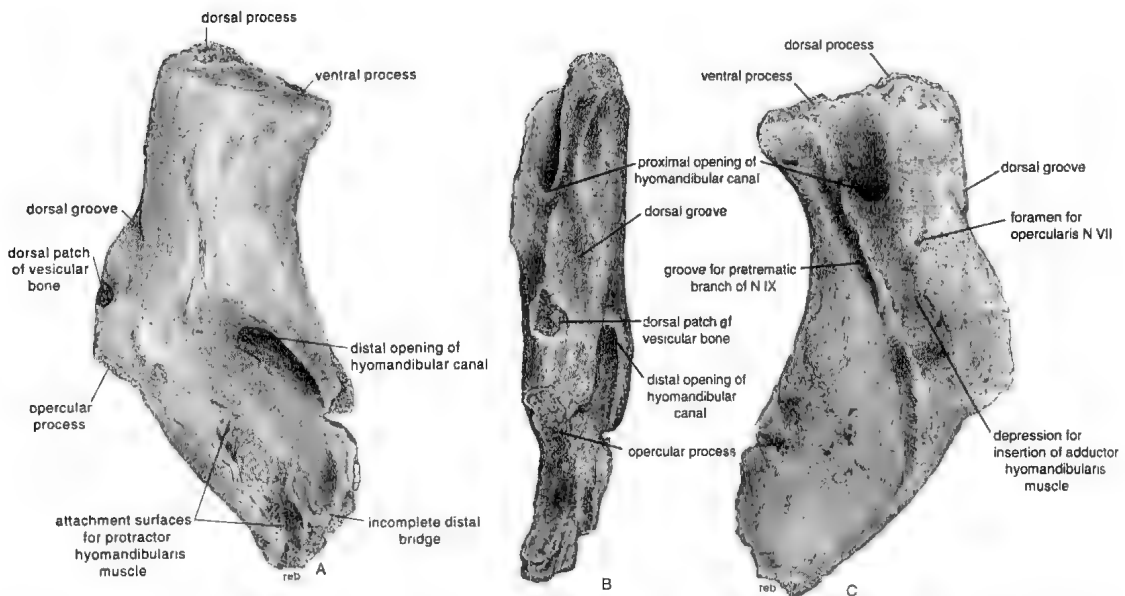


FIG. 44. *Cladarosymblema narrienense*. A-C, labelled reconstructions of the hyomandibular shown in Fig. 43, in anterolateral, dorsal and posteromesial views.

to which the articular is exposed on the posteroventral surface decreases with the age of the individual as the prearticular expands posteroventrally over its surface. A well-preserved mandible of *Gogonasus* to which we have access, is similar to our material, and has the separate bones more clearly defined. In this specimen a narrow strip of Meckelian bone extends along the entire ventral surface between the prearticular and the infradentaries, expanding again beneath the parasymphysial plate (Fig. 52D). This pattern is very similar to that in QMF21088 and 21102, a well-preserved mandible of *C. narrienense* in which the surface of the Meckelian bone clearly carries signs of the attachment of the posterior intermandibularis muscle (Figs 46D; 50C). This attachment surface is widest posteriorly where it is well-rounded in outline, and it gradually tapers anteriorly.

A pronounced postglenoid process is present behind the outer glenoid fossa. The dorsal surface of the process is usually poorly preserved, but it is covered with slightly roughened perichondral bone in the best-preserved individuals (Figs 49 C,F; 50B). Analogy with *Latimeria* suggests that the anterior mandibulohyoid ligament was attached to this dorsal face (Millot & Anthony, 1958: fig. 20), but Jarvik (1980: fig. 131) shows the depressor mandibulae muscle in the same position. On the ventral face of the post-glenoid

process two well-preserved specimens, QMF21087 and 31887, show a slightly vesicular surface (Fig. 46E), but many specimens show different amounts of bone removal, most of which is probably post-mortem (Figs 46D; 49B,E; 50C). However, in all specimens this ventral exposed scar-like surface is widest posteriorly and tapers anterolaterally. The scar is separated from the bone in front by a broad, deep and smooth furrow. A similar structure occurs in *Gogonasus*, although in that form the postglenoid process is not as large, and the furrow in its ventral face is smaller (Fig. 52D). The nature of the tissue attached to this ventral scar is difficult to determine. It could be that the posterior mandibulohyoid ligament encroached on the ventral face of the process, but this is far from certain and is in need of further research.

Internal Dermal Bones. The dominant dermal bone on the inner face of the jaw is the prearticular, which extends along almost its entire length but stops short of the median symphysis. It forms the internal rim and the mesial part of the anterior rim of the adductor fossa (Fig. 47A). As indicated above, the prearticular expands posteroventrally with increasing age of the specimen. At its anterior end it tapers to an acute angle where it is butted against the splenial and the Meckelian bone. Adjacent to the coronoids, it is slightly turned outwards to form a narrow flange. No-

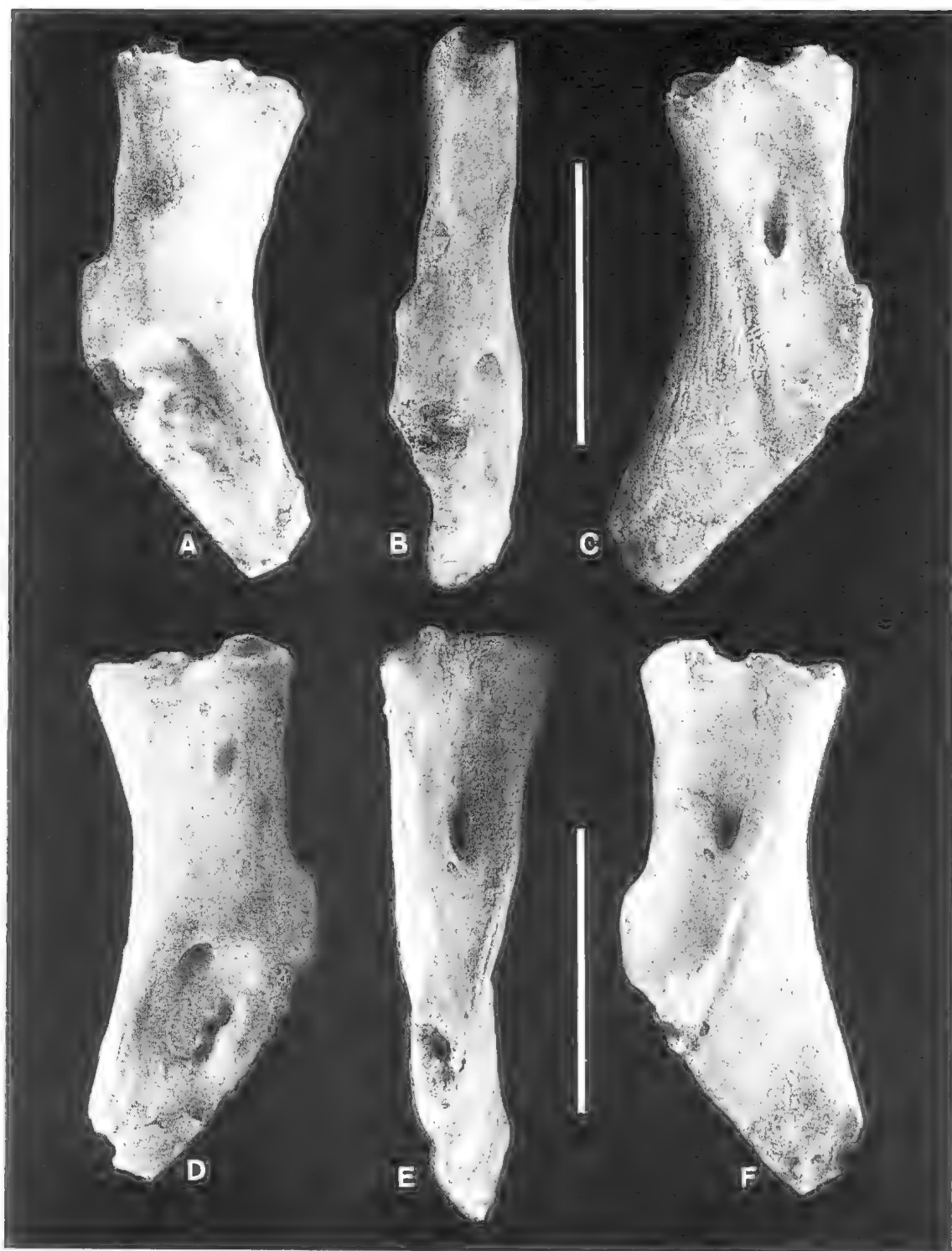


FIG. 45. *Gogonasus andrewsae*. A-C, anterolateral, dorsal and posteromesial views of the right, and D, E, F, of the left hyomandibular of ANU49259, for comparison with Fig. 43E-G. Scale: 10mm.

where is there a deep gutter between the prearticular and the coronoids as there is in *Gogonasus* (Fig. 52C). Ventrally, the prearticular lies against a narrow band of Meckelian bone which makes a distinctive support for the junction with the infradentaries. In the Meckelian bone, between the prearticular and the infradentaries, lies a deep groove for the articulation of the submandibulars and for the transmission of nerves and arteries (Figs 46D; 47A; 49E; 50C). This groove is shallowest and narrowest posteriorly, and deepest below the posterior end of coronoid 1; more anteriorly it remains broad but its inner edge becomes less well defined.

On all specimens regardless of size, the dorsal edge of the prearticular is embayed in front of coronoid 1 to form a large slightly elongated pit, the anterior mandibular fossa. This fossa has a well-rounded base and is floored by Meckelian bone, whereas variable amounts of coronoid, parasymphysial and infradentary bone make up its walls. Projections of these dermal bones into the outline of the fossa are present in several specimens (Figs 46B; 47A; 50D,E; 51A,B). Presumably the fossa received the vomerine tusk, but that cannot have been its only function because it has a vascular supply suggesting the presence of soft tissues. Such soft tissues could have been either ligaments or muscles that would have served to give stability to the flexible symphysis. Running anterodorsally from below this fossa to a point on the symphysis below the parasymphysial plate is a sharp, prominent flange (Figs 46B; 51A,B), the significance of which is not well understood, although it could have been for muscle attachment.

A second fossa, the intercoronoid fossa, which is shallower and more elongated in outline than the anterior mandibular fossa, also significantly embays the prearticular. It occurs in front of, and below, the tusk and replacement pit on coronoid 2 (Fig. 50D,E), and is lined with relatively smooth prearticular bone.

A broad and deep longitudinal depression occurs along the posterior half of the inner face of the prearticular at about its mid-height. On most specimens this depression or groove is devoid of denticles, and so probably its surface was not exposed in the buccal cavity; it must have been embedded in soft tissue. On QMF31864, however, the groove shallows out rapidly anteriorly and does carry denticles of reduced size (Fig. 50D). On all specimens, above this groove there is a flattened surface that is highest at the rear and tapers gradually to a position below the tusk on

coronoid 2, where it is deflected slightly ventrad before fading away in front of the tusk on coronoid 1. Posteriorly this surface lacks denticles, but about one-third of the distance along the adductor fossa, small denticles appear and rapidly increase in number anteriorly. They normally disappear anteriorly where the flattened surface fades away, but on QMF31864 they continue almost to the anterior end of the bone (Fig. 50D). Along the crest of the surface between the anterior end of the adductor pit and the tusk on coronoid 2 lies a row of slightly enlarged denticles that gradually disappear both anteriorly and posteriorly.

Three tusks (or tusk pairs separated by a replacement pit) and associated pits are present on all specimens, and so it is assumed that three coronoids are the norm for the species. The coronoids are well developed, and although the sutures separating them are not visible on most specimens, they can be approximated on QMF21088, where they are markedly zigzagged (Figs 46B,C; 47B). The boundary with the dentary is indicated on some specimens by a suture that shows as a discontinuous line of elongated pits. Coronoid 3 forms much of the anterolateral rim of the adductor fossa, meeting the prearticular at the mid-width of the rim and curving backwards to form a strip attached along the lateral wall of the fossa. The surface of each coronoid is highest laterally, falls away medially and, in adults, carries longitudinal ridges, particularly on coronoid 2. The lateral edge of each bone forms a low crest of variable height, and this normally lacks a row of denticles. It is deflected around the tusks, but on one specimen (QMF21099), a cluster of 6-7 teeth, some of which reach the size of the smallest dentary teeth, surmount this deflected edge on the posterior side of coronoid 1, and on QMF21089 three or four similar teeth lie adjacent to coronoid tusks 2 and 3. These structures are referred to as teeth rather than denticles, because at least some of them on QMF21089 have folded bases.

The floors of the pits immediately adjacent to the tusks all show radial ridges, indicating that they have been the sites of former tusks which have been shed. The radial ridges conform with the folding of the labyrinthine structure of the tusks and represent bone of attachment, as is shown by the sections dealt with in Histology (below).

Apart from the tusks and the few clusters of small teeth described above, the coronoids on most specimens do not carry any dental tissue.

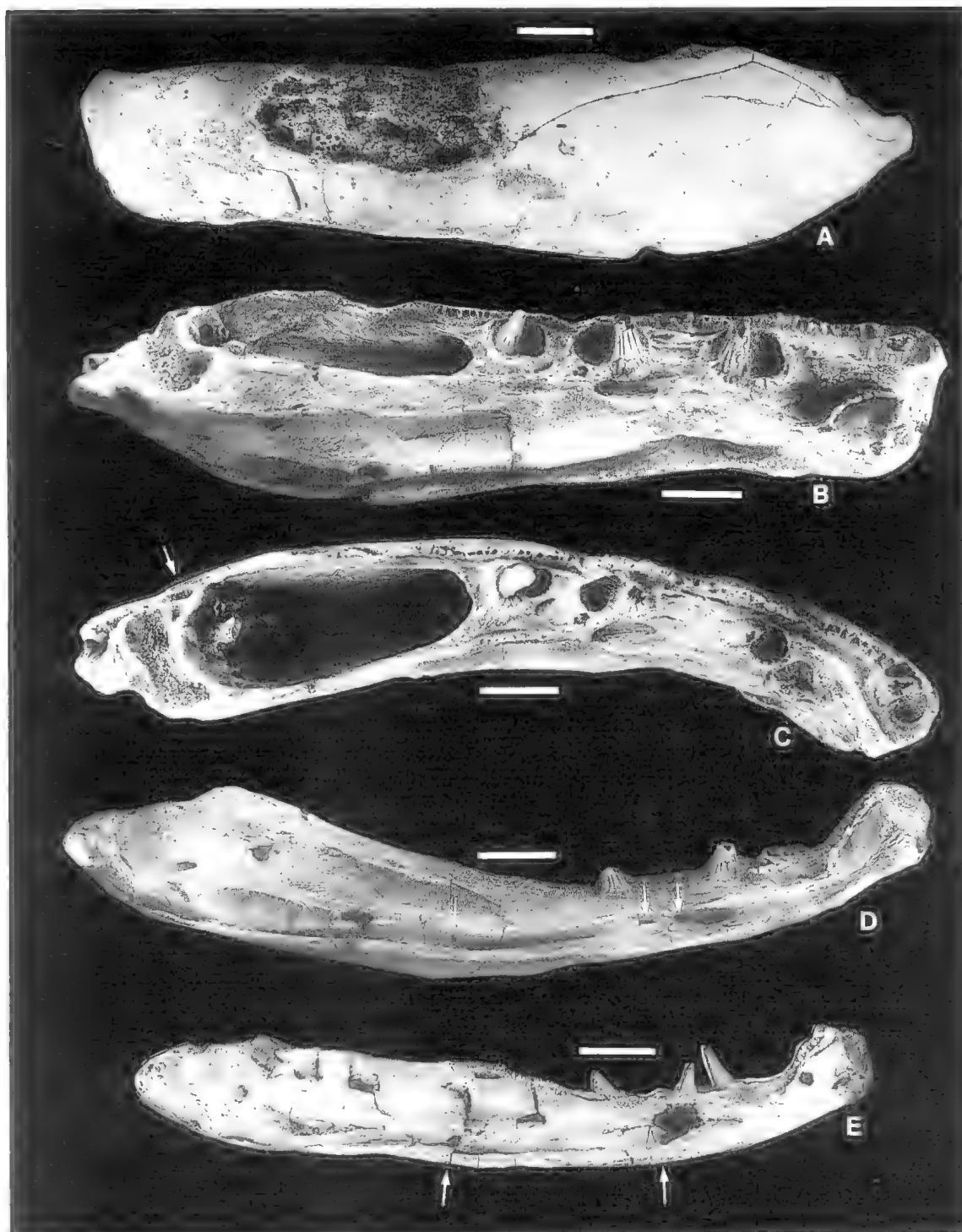


FIG. 46. *Cladarosymblema narrienense*. A-D, lateral, mesial, dorsal and ventral views of the best preserved left mandibular ramus, QMF21088. E, ventral view of left ramus, QMF21087. C, arrow indicates foramen for ramus mandibularis externus VII. D, E, arrows indicate major foramina in the submandibular furrow. Scale: 10mm.

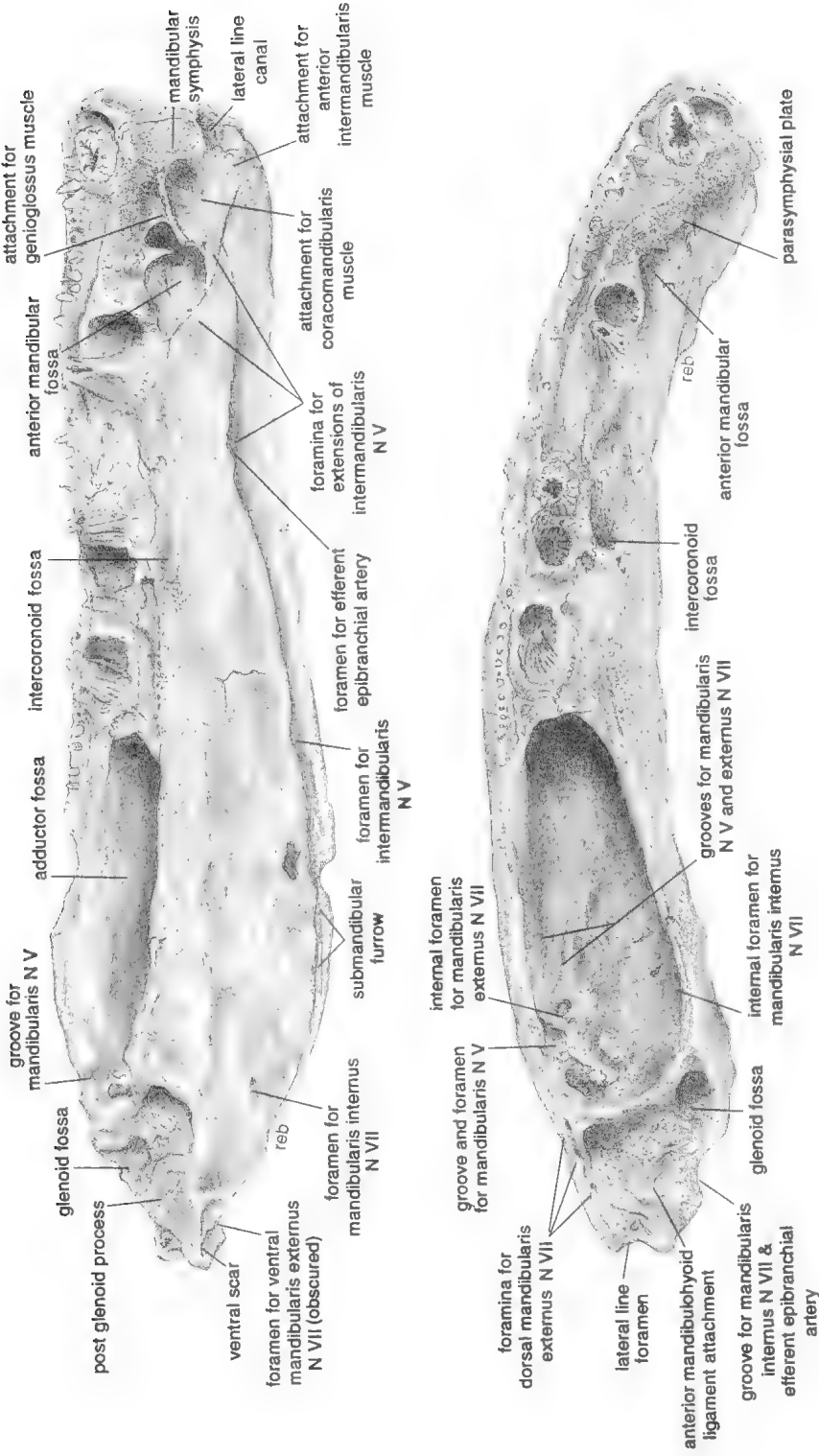


FIG. 47. A,B, labelled drawings of the specimen shown in Fig. 46B,C.

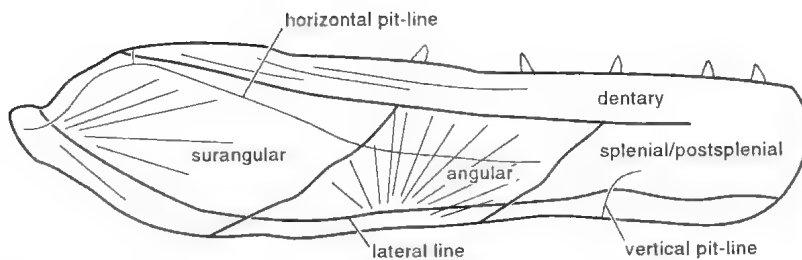


FIG. 48. *Cladarosymblema narrienense*. Outline drawing of external surface of a mandible showing bone boundaries, centres of ossification, pit-lines and lateral line canal. The radiation centres of the surangular and angular are derived from X-radiographs.

This arrangement is unlike that of *Gogonasus*, which is representative of the Osteolepididae in having a large number of denticles along the entire length of the coronoid crest, forming a continuous band with the denticles on the parasymphysial plate (cf. Figs 46C; 49C,F, with Figs. 52B,C).

In almost all instances the tusks and pits are paired, suggesting that as one is shed the adjacent pit gives rise to a new tusk. One distinctive specimen, QMF21087 (Fig. 50E), does not conform with this pattern. It has a tusk with two pits mesial to it on the dentary in front of the parasymphysial plate, two tusks with an intervening pit on coronoid 1, and a tusk on each of coronoids 2 and 3 separated by three pits, the middle one of which lacks radial ridges in its floor. Other variants usually involve paired tusks separated by a crowded pit on a single coronoid or on the front of the dentary. Around the bases of the tusks and the adjacent pits there is a raised ridge of bone, which in places shows a crenellated crest on the lingual side of the first and second coronoids (Fig. 46B,C).

Lying at the anterior end of the coronoid series is a transverse median plate with its lateral ends turned back above the pit for the vomerine tooth (Figs 46B,C; 47B; 50D,E; 57A-E). We refer to this as the parasymphysial dental plate, following Jarvik (1980). In some specimens the median edges of the left and right plates are seen to be finished, showing that they were not fused. This is an important point because the fact that the two rami always fell apart prior to burial, suggests that the symphysis was weak. That being so, the rami may have moved independently during mastication, a point supported by the strong double glenoid fossae (see Functional Interpretations below). The shape of the parasymphysial plate varies from specimen to specimen, but is always wide. In all except one small individual, its den-

ticulated surface bends posterolaterally and meets the coronoid 1 above the anterior mandibular fossa. The ventral edge of the plate lies on Meckelian bone, and its anterior side abuts the dentary. In most specimens the plate also extends ventrally to the oblique flange mentioned below, and in QMF21088, takes part in the formation of the dor-

sal part of that flange. The mass of vesicular bone that forms the main part of the symphysis (Figs 46B,D; 47A; 50D,E; 51A,B) and provides support for the central part of the plate, is composed of Meckelian bone that was probably completed by cartilage. In this *Cladarosymblema* is unlike the illustration and discussion of *Megalichthys hibberti* given by Watson (1926) and Borgen (MS), in which the prearticular is said to take part in the symphysis. The buccal surface of the parasymphysial plate is covered with small denticles; in some specimens it is bounded along the posterior edge by a row of significantly larger denticles.

Ventral to the parasymphysial plate, a sharp flange-like ridge curves obliquely downwards from the symphysis to the ventral edge of the anterior mandibular fossa (Figs 46B; 47A; 50D,E; 51; 58). Dorsally this ridge is formed of parasymphysial plate, but ventrally it is clearly Meckelian bone. On some specimens, this ridge has along its crest a number of flattened projections that are directed inwards and slightly downwards. A similar but much less prominent ridge occurs in *Gogonasus* (Fig. 52B,D,E). Ventral to the ridge is a relatively smooth surface of Meckelian bone that is overlapped to a variable extent by the infradentary ventral to it. This surface would have been a natural site for the attachment of large coracomandibularis muscles. Dorsolateral to the ridge the surface was possibly for the attachment of the genioglossus muscles (Jarvik, 1980: vol.2, fig. 117).

Immediately ventral to the surface for the coracomandibularis muscle attachment, the inner surface of the splenial is broad and roughened as though for the attachment of other muscles. This surface, which is well shown on Fig. 46B, extends posteriorly beyond the posterior edge of the anterior fossa. It was most probably for the attach-

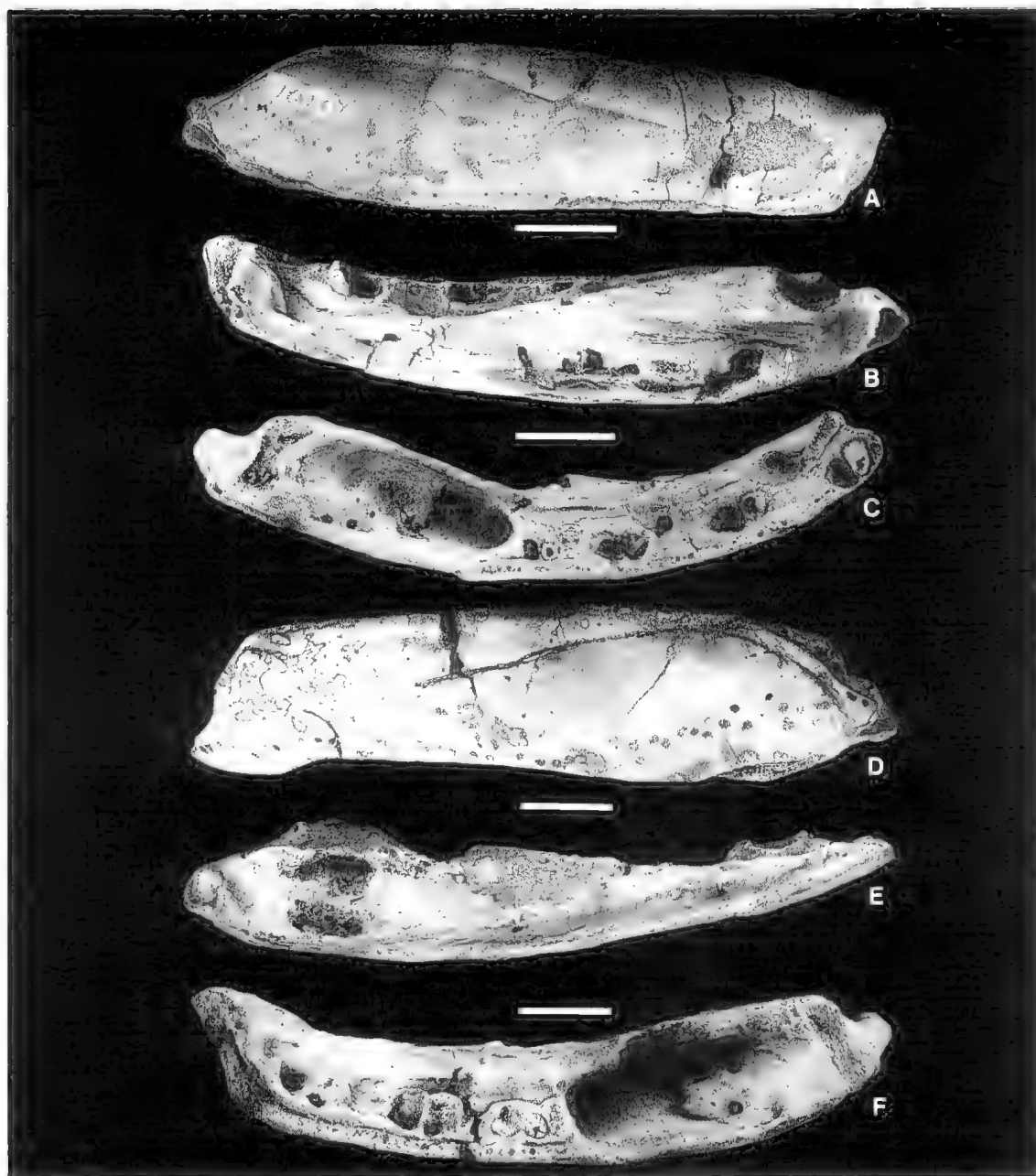


FIG. 49. *Cladarosymblema narrienense*. A-C, lateral, mesial and dorsal views of right mandible, QMF21101. A, showing row of pores for the mandibular lateral line canal and cosmine resorption towards the anterior. B, showing the anterior end of the prearticular, upturned edges of the external dermal bones immediately ventral to it, and the deep furrow anterior to the postglenoid process leading into a sharply defined furrow for the ramus mandibularis internus VII (arrow). C, showing the large postglenoid process, the pair of foramina in the lateral wall of the adductor fossa, and the regular tusk and replacement pit pairs. D-F, lateral, ventral and dorsal views of a left mandible, QMF21090, with its anterior end eroded away. D, showing unusually strong pit-lines and lateral line pores, and some unusual cosmine blisters anteriorly. E, showing the submandibular furrow; arrows indicate foramina in submandibular furrow. F, showing two foramina in the lateral wall of the adductor fossa, and an anomalous arrangement of tusks and replacement pits. Scale: 10mm.

ment of the anterior intermandibularis muscles. A similar, but much larger surface, is present in *Gogonasus* (Fig. 52B).

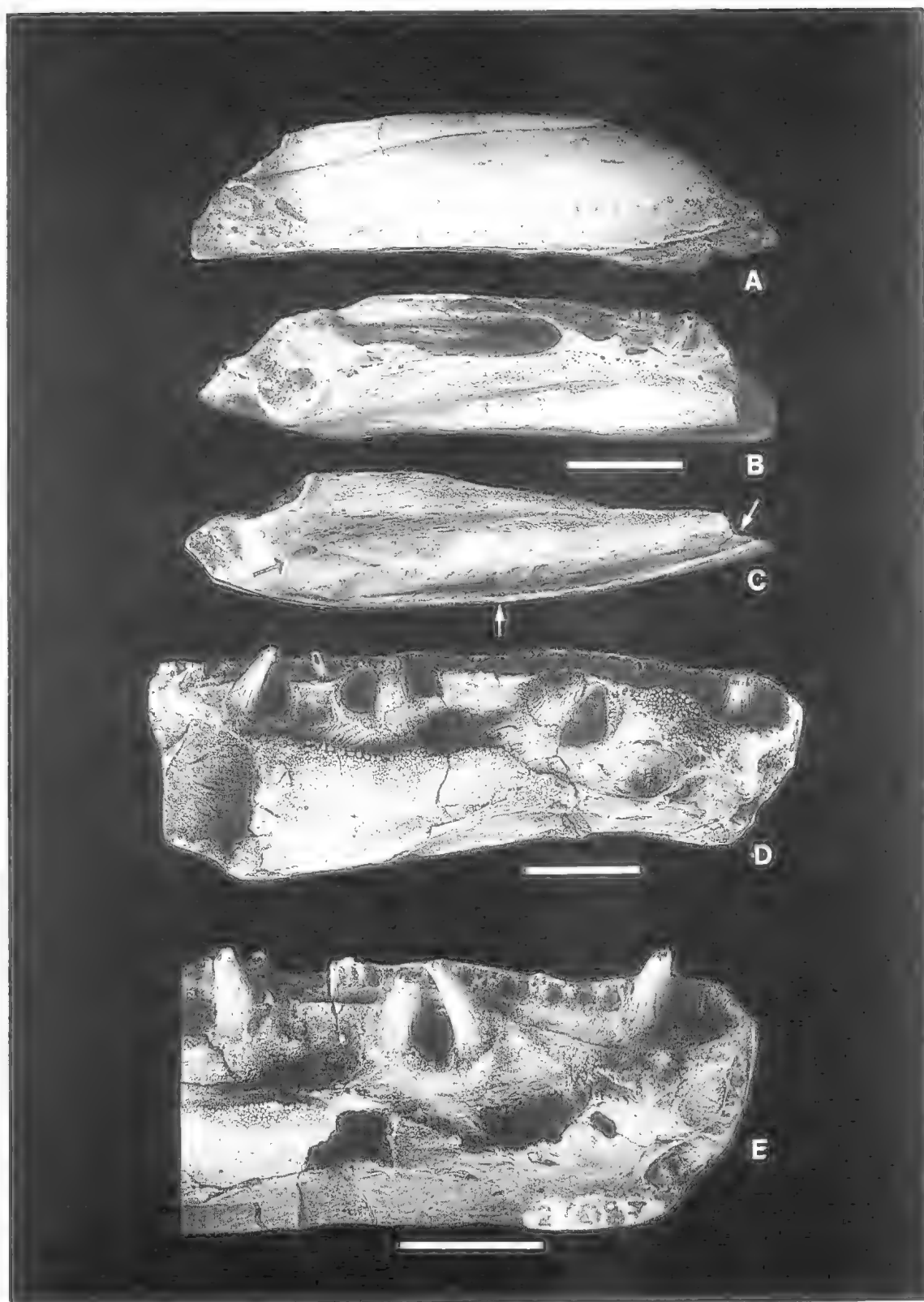
Grooves and Foramina. We are aware of no osteolepiform mandibles showing this degree of detail having been described. Gross (1941) described details of the grooves and foramina in some incomplete *Panderichthys* and several porolepiforms, but he was cautious about their interpretation. Jarvik's interpretation of the foramina in the mandible of *Eusthenopteron* is partly based on his views of the evolution of the tetrapod ear (Jarvik, 1980: Vol.2, figs 97-100), some aspects of which we do not find convincing. Hence we have had to fall back on data from extant sarcopterygians, such as *Neoceratodus* and *Latimeria*, and the basic knowledge of the nerves and vessels that occur in the mandibles of all primitive osteichthyans, for our interpretations. These are: the mandibularis V₃ and its branches such as the intermandibularis, which are motor nerves to the various muscles of the throat and the sensory structures of the symphyseal region; the mandibularis externus and internus VII, which are sensory nerves to the internal and external surfaces of the mandible; the lateral line nerve to the mandibular lateral line; the efferent epibranchial artery; the hyoid artery; and the mandibular vein. The positions of these structures are comparable throughout all the groups of primitive fishes, and this gives us some confidence in the identification of grooves and foramina. However, we acknowledge the possibility of contrary evidence. In the following description, we deal first with those features that are uniform in their distribution in available specimens and can be confidently interpreted, and then move to more variable and obscure features.

On all specimens, the lateral line canal enters the mandible just behind the articulation and between the postglenoid process and the posterior tip of the surangular. The foramen is obvious, and the canal from it runs anteroventrally as is shown by the lateral line pores and the X-radiographs (Fig. 54A,B).

A groove of variable depth occurs between the articular and the dorsal edge of the surangular, and on most specimens runs into a small foramen (or a group of small foramina) between these two bones a few millimetres further forwards (Figs 46C; 47). This opens into a tube that issues through a distinct foramen between the articular and the surangular in the posterolateral wall of the adductor chamber. As is shown on QMF31861, this tube is quite expansive and has one or two small offshoots which seem to end blindly (Figs 55D; 56B), but are more probably connected to very small foramina on the posterior surface of the mandible between the articular and the surangular. The identity of the nerve occupying this canal and groove can be determined from its position and orientation. Although it enters the mandible anterior to the glenoid fossa, and is therefore in a position appropriate for mandibularis V₃, it is clear that the nerve impinged on the mandible from a posterodorsal direction, and therefore it is likely to be a branch of the facialis nerve VII. In that position, the only such branch would be from mandibularis externus VII. Gross (1941) observed a tube in this position in sections of *Glyptolepis baltica* and *Panderichthys rhombolepis*, and labelled it as the canalis articularis, although he did not assign a function to it. He also believed that this tube opened in a posteroventral position, as does the one dealt with in the next paragraph. Consequently his canalis articularis may have been connected to both dorsal and ventral foramina.

Another groove of variable depth extends along the ventral contact between the articular and the surangular into the submandibular groove. A short distance from the posterior end of the articular a branch enters a foramen that connects with a tube that lies between the surangular and the articular, and connects with a large foramen in the posterolateral wall of the adductor chamber. This canal, which is well displayed in Figs 55D, 56B & 57G, has several anteroventrally directed branches that open through foramina low on the posterior wall of the adductor chamber, in addi-

FIG. 50. *Cladarosymblema narrienense*. A-C, lateral, mesial and ventral views of small left mandible, QMF21102. A, showing unusual sharp flexure in row of lateral line pores. B, showing face of prearticular and distribution of denticles on its surface, some of which have been removed during preservation, leaving pits. C, showing posterior foramen and incomplete edge of the anterior foramen in the submandibular furrow (external arrows), the furrow anterior to the postglenoid process, and the foramen for the mandibularis internus VII (internal arrow). D, mesial view of the anterior half of a left mandible, QMF31864, showing shape of anterior end of the prearticular, distribution of denticles on its surface, shape and denticulation of the parasymphysial plate, and anterior and inter-coronoid fossae for reception of tusks from the upper jaw. E, mesial view of QMF21087. Note the same features as in D, and the two tusks with an intervening replacement pit on the anterior coronoid. Scale: 10mm.



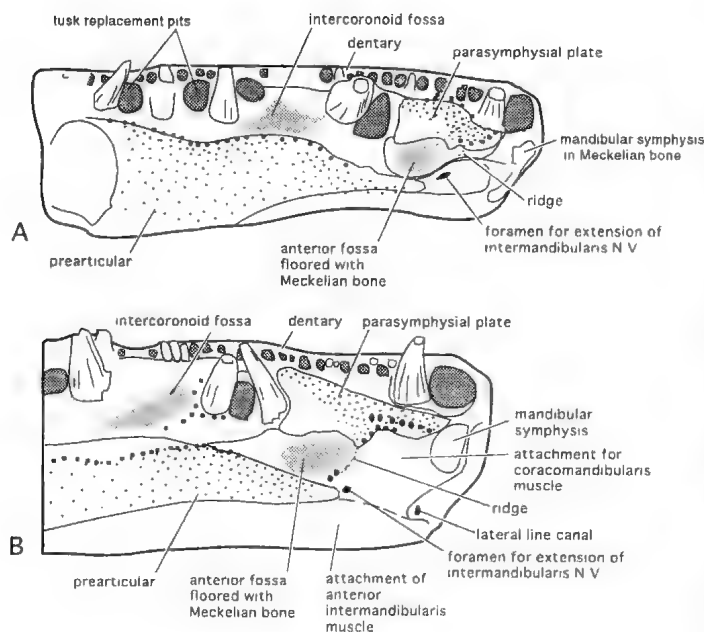


FIG. 51. A, B, labelled key to Fig. 50D,E.

tion to the main branch, which opens higher on the internal face of the surangular. The subsidiary branches vary in number between specimens. The fact that this system lies lateral to the ossified Meckel's cartilage shows that it cannot have carried a vessel, and so it must have been a nerve. This nerve must have passed behind the jaw articulation from a posterodorsal direction, and the only nerve to enter the mandible from that direction is the facialis nerve VII. It is therefore most probably the ventral branch of the ramus mandibularis externus VII.

A constricting groove passes around the posteromesial surface of the postglenoid process of the articular on to its ventral surface. Although the connection is not completely clear on most specimens, one small individual, QMF21102, shows definitely that at least part of whatever occupied this groove passed anteriorly into a smaller groove that enters a foramen within the articular (Figs 49B; 50C; arrows). From this fo-

ramen, a tube runs anteriorly within the bone and opens into the posteromesial wall of the adductor chamber. Thence a groove runs forward along the inner wall of the prearticular; although its course is difficult to illustrate, it can be traced at breaks in the bone and on the internal surface of dissected specimens. Occasionally a branch of this groove opens through a foramen between the prearticular and the coronoid. These foramina and grooves are appropriately placed to transmit fibres of the mandibularis internus VII (chorda tympani). In *Amia* (Jarvik, 1980: 71) that nerve serves the mucous membranes on the buccal surface of the mandible. In addition, numerous small foramina on the inner surface of the jaw high on the prearticular and along the junction with the coronoids, probably carried fibres of the mandibularis internus VII. Jarvik (1980: vol. 2, fig. 97)

showed a foramen on the external surface of *Eusthenopteron* in the same position as the one we are considering. However, he believed that it connected via a tube in the articular with a foramen on the lateral side of the adductor fossa, and that it transmitted a branch of the auriculotemporalis V nerve from the anterior to the posterior. No such tube exists in *Cladrosymblema*; nor can we find a foramen in the position he indicated for the chorda tympani (mandibularis internus). Gross (1941) noted a foramen entering a tube at the same position as in *Cladrosymblema* in *Glyptolepis baltica*, and referred to it as the canalis prearticularis. He claimed that it carried a blood vessel, a view with which we have to disagree.

The main constriction around the posterior end of the postglenoid process, referred to in the last paragraph, is much too large to have carried the ramus mandibularis internus VII only, and it is

FIG. 52. *Gogonasus andrewsae* Long. All figures of right mandible, ANU49259. A, lateral view. Note increase in height towards anterior and large isolated pores and intervening smaller pores for lateral line canal. B, mesial view. C, dorsal view. Note strong furrow along outer edges of coronoids, and weaker one along their inner edges; and the two foramina in the outer wall of the adductor fossa. D, ventromesial view showing abrupt anterior termination of the prearticular and broad submandibular groove with multiple foramina. E, enlargement of symphyseal region in mesial view. Note continuous band of denticles on the parasymphysial and coronoid plates, the very broad band of external dermal bone exposed on the inner ventral surface for attachment of anterior intermandibularis muscles, and shape of symphyseal junction. Scale: 10mm.



likely to have been occupied by a major vessel. In such a position this would have been the hyoid or the efferent epibranchial arteries or both. They would have been distributed in the soft tissues along the inner face of the mandible, including the various sub-branchial muscles.

In the submandibular furrow between the infradentaries and the Meckelian bone, there is one large foramen and, in some specimens, one or two smaller foramina lying in the deep embayment below the postsplenial or the angular. The large one passes up through the bone (Figs 46D,E; 47A; 55B) and joins a groove that runs from a posterodorsal direction past the foramen and thence along the floor of the Meckelian cavity (referred to by Gross, 1941, as the *canalis primordialis*) inside the submandibular furrow. As indicated below, we consider that this foramen transmitted the ramus intermandibularis V from the Meckelian cavity to the submandibular furrow. However, it probably also transmitted a branch of the efferent epibranchial artery from the exterior to the Meckelian cavity. This artery passed around the posterior end of the mandible in the groove as described above.

On the external surface, a groove continues in the submandibular furrow towards the anterior end of the mandible (Figs 46D,E; 49E; arrows), where it divides. The ventral branch runs to the symphysis and the dorsal one runs up into a foramen situated either in the splenial or in the plate of Meckelian bone (Figs 46B; 47A; 50E; 51 A,B). This foramen and its connections are described in detail in the next paragraph. The implication is that a nerve or a vessel, or both, supplied the soft tissues in the anterior part of the Meckelian cavity and the muscles attached in the region of the symphysis.

QMF31860 shows that within the symphyseal region the foramen joins with a perichondrally-

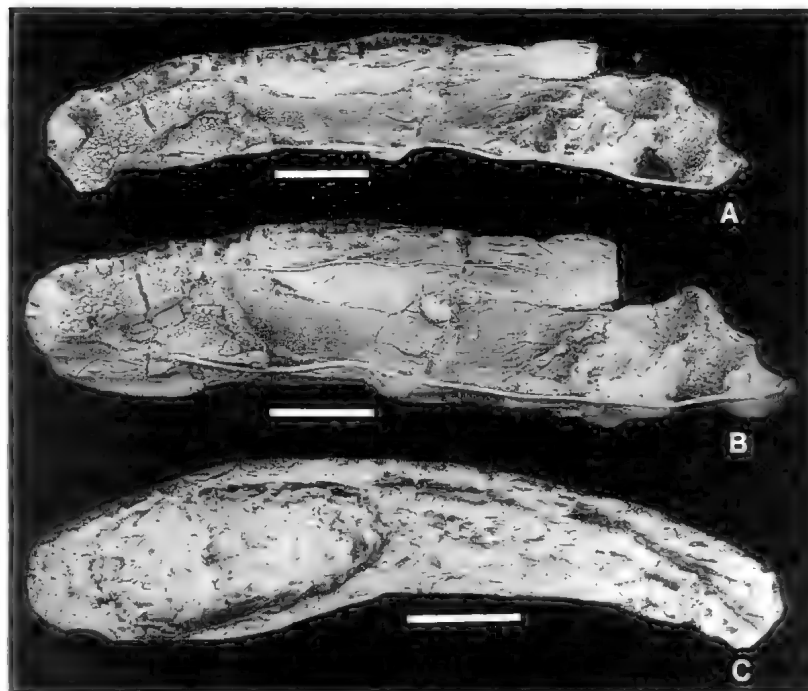


FIG. 53. *Ectosteorhachis nitidus* Cope. A, B, dorsal and mesial views of right ramus, MCZ8827. Note strongly denticulated parasymphysial plate and denticulated anterior end on the prearticular. The weakly represented radiation centre on the inner surface of B suggests that the surangular is large and its centre of ossification is posteriorly situated as in *Cladarosymblema*. (The threads along the dorsal and ventral inner surface have been cemented in place to strengthen the specimen.) C, dorsal view of MCZ8826. Most of the teeth and tusks on the coronoids were removed during the original preparation, but the strong groove between the dentary and the coronoids remains. (These specimens were among those used by Thomson, 1964a: fig. 4.) Scale: 10mm.

lined groove that is impressed on the inner face of the infradentaries, and runs in an anterodorsal direction towards the symphysis (Figs 57C; 58). This is just one of several similar grooves in the Meckelian lining of the external dermal bone. The others enter the symphyseal region from the Meckelian cavity. The main tubes branch and interconnect, and at first sight they seem to represent passages for nerves rather than vessels. For this reason, we conclude that the anterior as well as the posterior part of the submandibular furrow carried nerves as well as arteries. Such nerves would be extensions of intermandibularis V. Those in the Meckelian cavity would have been mandibularis VII. However, an alternative has to be entertained because we can find no external openings connecting with these grooves, and they do not connect with the lateral line canal. We can only conclude that whatever they carried ramified into the bone spaces, suggesting that they carried nutrients rather than nerves. Until sufficient ma-

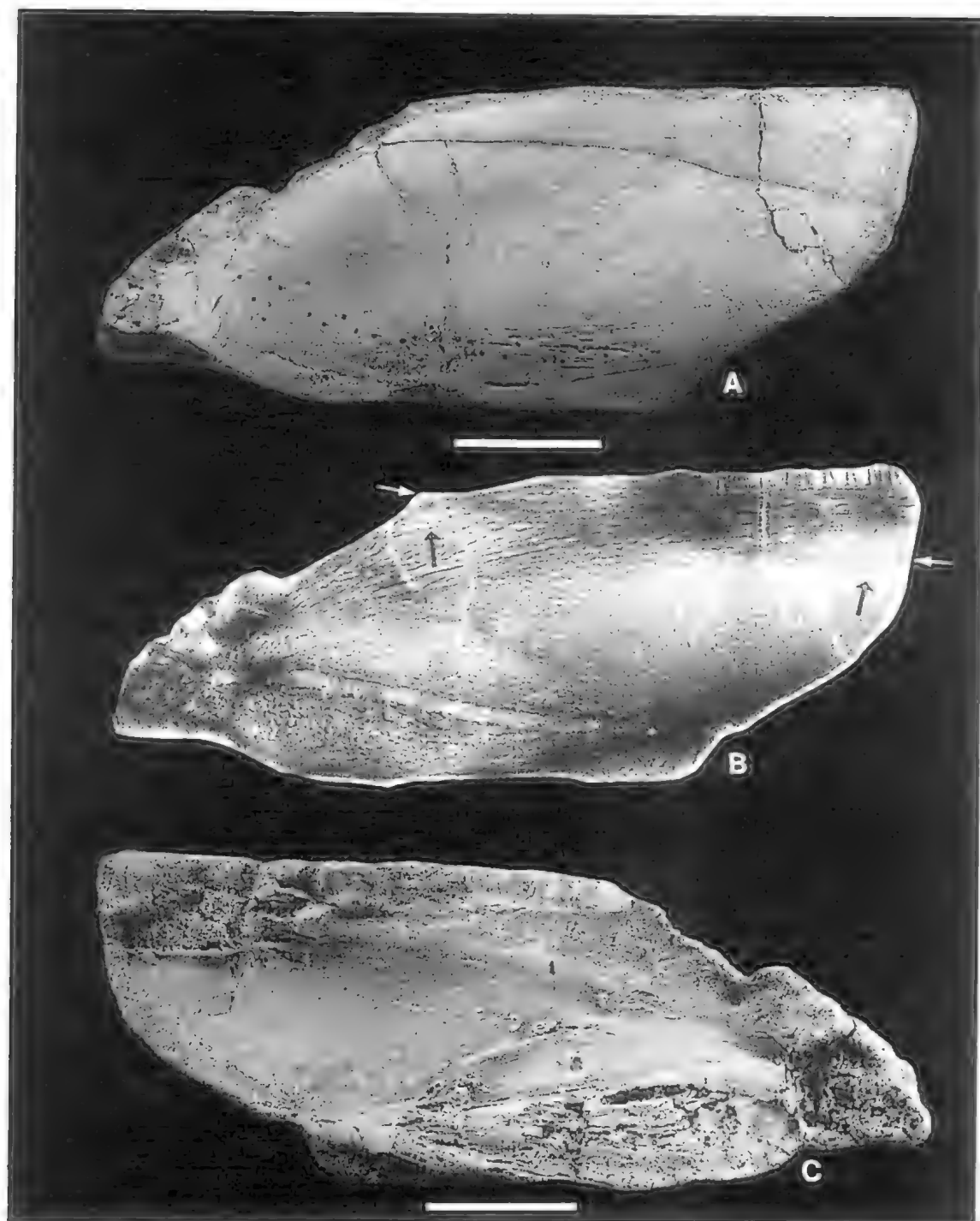


FIG. 54. *Cladarosymblemanarrienense*. A, C, exterior and interior views of posterior part of external dermal bones of an incomplete mandible, QMF21100. B, X-radiograph of same. Note position of lateral line canal, ossification centres of angular and surangular, and horizontal pit-line. In particular, note the anterior and posterior divergence between the boundary between the dentary and infradentaries (horizontal arrows) and the horizontal pit-line (vertical arrows). Scale: 10mm.

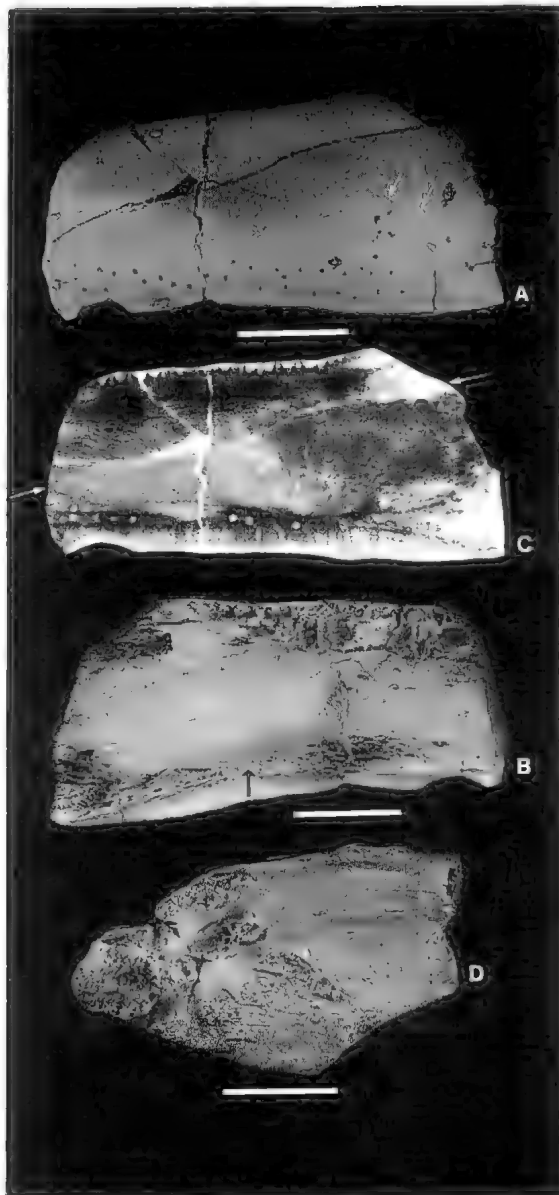


FIG. 55. *Cladarosymblema narrienense*. A, exterior view, external bones of part of mandible, QMF31867, showing lateral line pores, horizontal pit-line, and *en echelon* furrows (white arrows) marking approximate position of suture between angular and surangular. B, Interior view of same with the radiation centre of angular and superimposed foramen in submandibular furrow. Arrow marks position of foramen for intermandibularis V and possibly efferent epibranchial artery. C, X-radiograph of same in orientation of A; interpreted in Fig. 56A. Arrows indicate horizontal pit-line. D, internal view, posterior part of external dermal bones, QMF31861, showing various canals discussed in the text, and interpreted in Fig. 56B. Scale: 10mm.

terial becomes available to permit sectioning, their function will remain unknown. Gross (1941) also observed foramina and tubes entering the anterior part of the submandibular furrow in several of the genera he discussed, and referred to them as 'Känale im Medialrand des Mentomandibulare'.

Within the adductor chamber of QMF21101 and 21090, immediately dorsal to the previously mentioned main foramina for the mandibularis externus VII (Fig. 49C,F) are one or two foramina that are vertically directed. In other specimens no such foramina exist, but a shallow groove runs steeply down in front of the mandibularis externus foramen; this is continued anteroventrally as a pronounced groove along the junction between the articular and the infradentaries, and then directly anteriorly. In the floor of the forward extension there are four or five foramina, some of which may penetrate the bone to exit in the submandibular furrow, as has been discussed above. Some of them do not penetrate the bone and presumably serve the sensory structures in the bone. This system was probably for the mandibularis V, which entered the mandible through the posterior part of the adductor fossa. The foramina in the submandibular furrow are appropriately placed to have carried nerves to a sheet of muscle such as would be expected if they innervated the intermandibularis muscles. The main branch of this groove opens at a foramen in the submandibular furrow just below the ossification centre of the angular, and we consider that it carried the main branch of the ramus intermandibularis V. This interpretation would be consistent with the inferred position of the intermandibularis muscles served by this nerve. An entirely similar arrangement is present in *Gogonasus*, in which two other small foramina can be seen passing through the bone to enter the internal groove a short distance behind the main one.

The mandibular vein has not been discussed. We surmise that it joined the lateral venous sinus via the adductor fossa, and thence joined the orbital venous sinus, leaving no trace on the bone.

The adductor fossa is long and wide, its proportions changing slightly with age. The width/length ratio is 0.38 in the smallest specimen, and 0.46 in the largest.

Comparison with the Mandible of Ectosteorhachis. We have examined MCZ8826-8827 which, with MCZ8641, formed the basis of the description by Thomson (1964a: fig. 4). The specimens are figured herein as Fig. 53A-C.

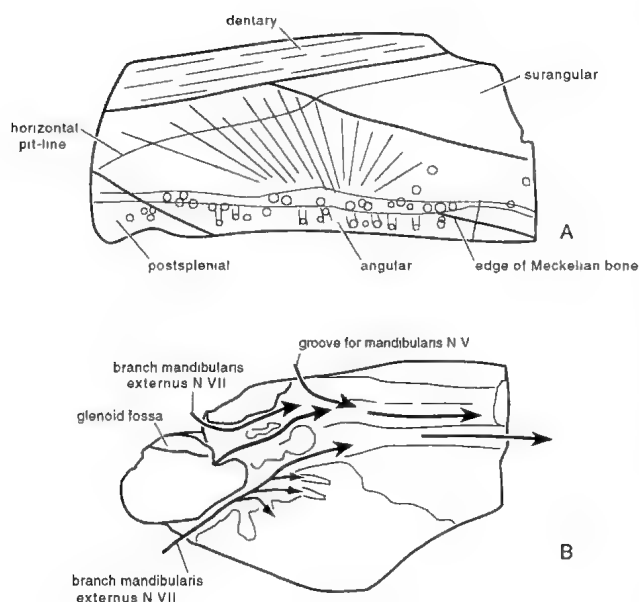


FIG. 56. *Cladarosymblema narrienense*. A, key to Fig 55C. B, key to Fig. 55D.

Firstly, we note that MCZ8827 is extensively crushed, and MCZ8826 is otherwise damaged, making it difficult to recognise the sutures shown on Thomson's diagrams, particularly those between the infradentaries. In our view there is no evidence that the splenial terminates behind the symphysis, as shown by Thomson (1964a: fig. 4A); in that region the arrangement of the dermal bones is no different from that of other osteolepiforms. The suture along the ventral edge of the dentary is strong and shows finished edges to a wide groove along parts of its length; it cannot be traced as far forwards as Thomson shows, but posterodorsally it leaves a broad band, as in his fig. 4A. This band is proportionately much larger than in any specimen of *C. narrienense*.

The posterodorsal edge of the mandible is naturally truncated, and exposes a large segment of articular bone in lateral view. This implies that the subopercular 1 overlapped the mandible to a greater extent than in *C. narrienense*, and that the submandibulars did not reach as far posteriorly as in that species.

We see no evidence to support the existence of three pairs of coronoid tusks in *Ectosteorhachis*. There is a strong gutter between the coronoids and the dentary, and more than one row of large

denticles along the outer rim of the coronoids (Fig. 53C). Large denticles are also present on the preserved anterior part of the prearticular in MCZ8827, although MCZ8826, which has the prearticular preserved, has had the large denticles stripped from all but a few patches during the original preparation.

The structure labelled 'crista dentalis' by Thomson (1964a), and said to be (p. 291) '... an enlargement of the anterior rim of the anterior dentary fossa', and (p. 302) 'a denticulate ledge' of the dentary, is really the parasymphysial plate (Fig. 53A,B); it is clearly a separate bone, the suture with the Meckelian bone behind and with the dentary in front, both being evident. The denticles on its surface are comparable in size with those on the prearticular, being much larger than those in equivalent positions in *C. narrienense*.

The glenoid fossa is transverse and double, unlike the representation given in Thomson's figures 4B&C. Although the preparation is not good enough to be certain of the point, it seems that the fossa is of the standard osteolepiform type. On MCZ8826 there is a definite postglenoid process that has been partly destroyed during the original preparation. Its lateral periosteal surface is clearly cut through, and the vesicular bone structure is still clearly visible on the other surfaces. On MCZ8827, part of the dorsal surface of the process is still present. Although examination of Thomson's illustrations may suggest that the reduction of this process may be useful in differentiating *Ectosteorhachis* from *Megalichthys*, examination of the specimens shows that this is not possible.

The adductor fossa is wide in comparison with that of *C. narrienense*; its proportions on MCZ8826 are original, and not the result of distortion.

Although its preparation does not permit the accurate identification of most foramina, MCZ8826 does show one feature very clearly. Lateral to and just in front of the glenoid fossa is a group of ten tubules filled with iron oxides. These tubules run ventrally from openings in the blade of the surangular, converging as they go. At first they join into twos or threes, and presumably in a more ventral position they coalesce com-

pletely, although that position is not exposed. In *Gogonasus* and *Cladarosymblema*, only one to three foramina instead of ten occur in this position. As indicated above, we have concluded that the foramina transmitted the mandibularis externus VII nerve.

Apart from the denticulated ridge on the lateral margins of the coronoids, and the possibility of the presence of only two coronoids, we see no evidence from the mandible to permit the separation of *Ectosteorhachis* from *Megalichthys*, although we note that many details of the former genus remain obscure. We note also that the new genus described from Norway by Borgen (MS), is comparable with *Ectosteorhachis* in its denticulated marginal coronoid ridges, and possibly in having only two tusk-bearing coronoids. Separation of *Ectosteorhachis* from *Cladarosymblema* can be made on the basis of the wide adductor fossa, the gutter between the dentary and the denticulated coronoid ridge, the size of the parasymphysial plate, and the size and abundance of the denticles on that plate and the prearticular. We note, however, that all these distinctions rest on an inadequate sample of *Ectosteorhachis*.

PECTORAL GIRDLE

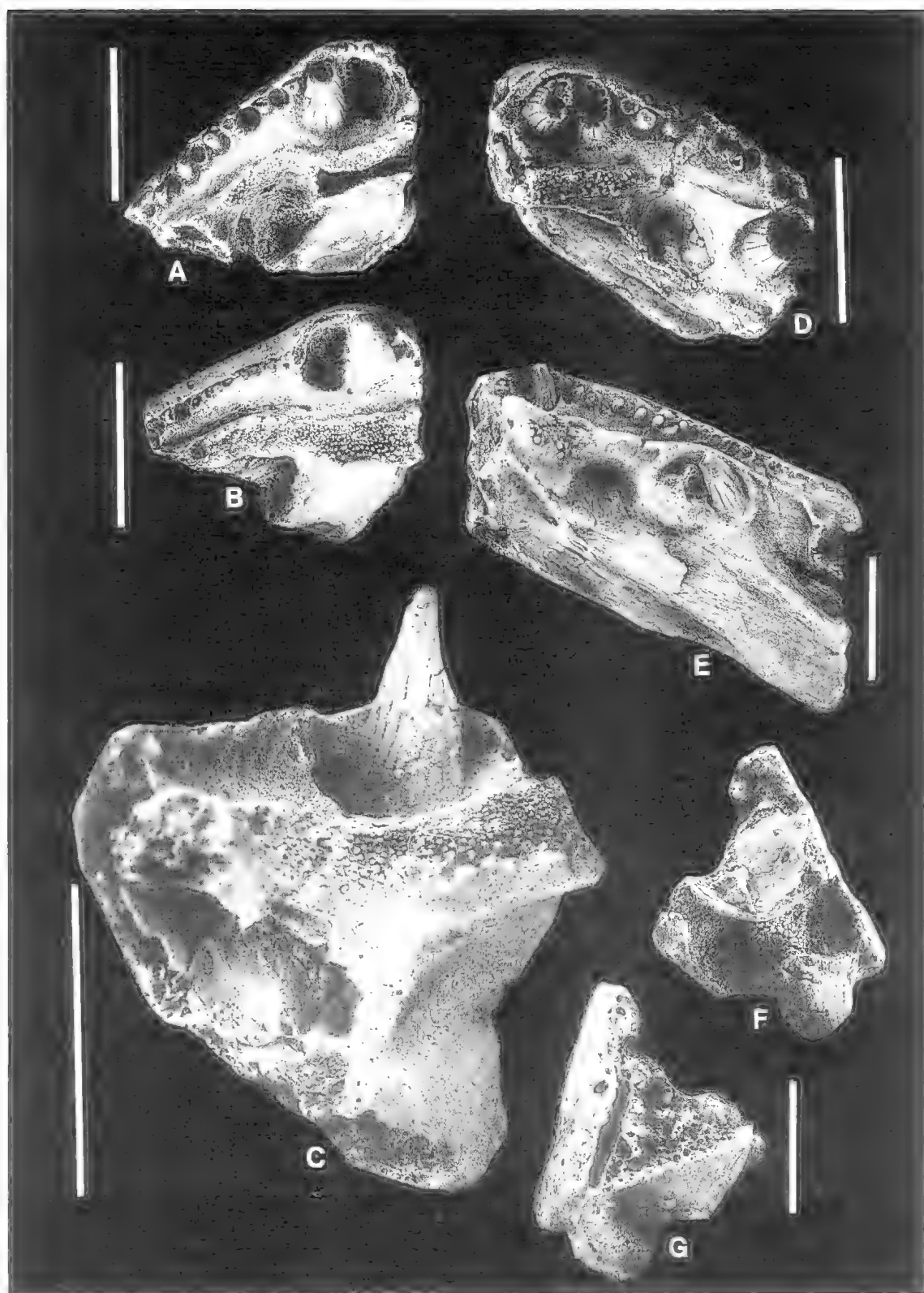
The pectoral girdle is known from one complete supracleithrum (Fig. 59A,B), two broken anocleithra (Fig. 59C,D), three broken cleithra (Fig. 60A,B,E), one isolated almost complete clavicle (Fig. 60F), an almost complete cleithrum and clavicle from one individual (Fig. 61A-C), the incomplete clavicles of the holotype, and two partly crushed scapulocoracoids still attached to the isolated cleithra (Figs. 60B; 61A). Because other genera are represented in the etchings, it is necessary to establish that these specimens belong to *Cladarosymblema*. We have concluded that they are properly assigned for the following reasons. The exposed part of the clavicles of the holotype, though poorly preserved, are largely covered with a network of raised ridges rather than cosmine. The same is true of what we regard as fragments of the cleithra of the holotype. In addition, one of the isolated fragmentary cleithra

has cosmine on its posteroventral corner, and another has patches of cosmine near the broken dorsal extremity of the bone. These isolated bones have a pattern of ridges on the external surface. The external surface of the anocleithrum and supracleithrum also have the distinctive pattern of ridges, and patches of cosmine in similar relationships. As Jarvik (1948) has pointed out, the cosmine-bearing *Osteolepis* itself has variably ridged surfaces on parts of the pectoral girdle along with cosmine. Its ornament differs from *Cladarosymblema* in the relative extent of the two types of surface.

Supracleithrum. This is represented by a single complete bone (QMF31859) from the right side (Fig. 59A,B). Its exposed surface has a tracery of fine ridges, similar to those on the posterodorsal part of the anocleithrum, and a small patch of cosmine at the posterior extremity. Two types of overlapped surface are recognizable; a large well-defined surface through which the lateral line passes, and which is traversed by branching radial grooves and some pits; and a much narrower strip along the anteroventral edge differentiated from the exposed surface by a distinct change in slope. The former was overlapped by the posttemporal and the latter by the opercular.

Anocleithrum. This bone is represented by two fragments (QMF26555, 31862), one from each side of the animal (Fig. 59C,D). The right one was partly destroyed during photography, but the left one was incomplete when found; both are robust. The exposed part has a tracery of ridges over the posterodorsal surface, decreasing in size posterodorsally, and a patch of cosmine posteriorly. The ridges carry a row of small pustules. The overlapped surfaces are extensive, and the anterior process is twice the size of that of *Osteolepis* (Jarvik, 1948: fig. 25). The process of the left bone (QMF31862) is complete; its anterior end is rugose and carries a vascular groove on its ventral edge. On its outer face is a sharp crest that marks the edge of the cleithral overlap, and so the tip probably represents the attachment of a ligament. The area overlapped by the cleithrum indicates

FIG. 57. *Cladarosymblema narrienensis*. A,B, symphyseal parts of the left rami of two mandibles, QMF31869 and 31860, showing the tusks and replacement pits, the parasymphysial plates, and the variable arrangement of the marginal teeth in relation to the edge of the jaw anterior to the tusks. C, enlargement of B viewed from a posterolateral direction; for interpretation, see Fig. 58. D-E, symphyseal parts of right rami of two mandibles, QMF31865, 31868, showing similar features to A-C, but with two anterior tusks in D, and two tusks in the anterior coronoid as well as the abbreviated area of denticles on the parasymphysial plate of E. F,G, posterior end of a right ramus, QMF31887, in dorsal and ventral views. F, showing double glenoid fossa and the rounded postglenoid process. G, has been eroded to expose the tube for the ramus mandibularis externus N VII. Scale: 10mm.



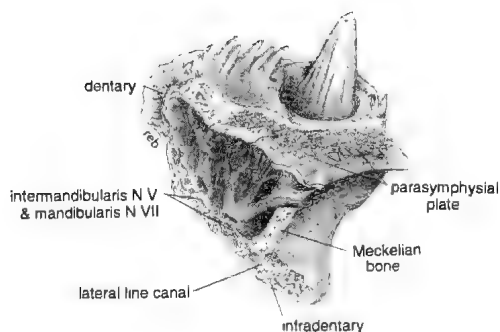


FIG. 58. *Cladarosymblema narrienense*. Reconstruction of the specimen shown in Fig. 57C to show the tubes servicing the symphyseal region.

that the dorsal edge of that bone is truncated, but with its ends rounded off.

Schultze (1987: 69), commenting on the work of Rosen et al. (1981), indicated that 'the character "anocleithrum without surface ornamentation" cannot be evaluated because the condition of the anocleithrum is not known in plesiomorphic dipnoans, or rhipidistians'. This is difficult to understand because the anocleithrum was buried and unornamented in the several Devonian dipnoans in which the bone is known; and Jarvik (1980) has figured a highly ornamented anocleithrum in *Eusthenopteron*. Jarvik (1985) and Long (1985b) have listed an ornamented anocleithrum as a distinctive feature of osteolepiforms. The presence of ridged ornament and cosmine on the anocleithrum of *Cladarosymblema* puts the matter beyond doubt.

Cleithrum. This bone (QMF26548, 26554, 26563, 26564, 26572 and 31875; Figs 60A-E; 61A-C) is robust and survived the preservation processes well. It is thin around the dorsal and posterior edges, but thickens considerably towards the anterior and ventral edges. In posterior profile, the upper part of the bone is almost planar, but the lower planar part is inflected at an angle of c.130°, and twisted slightly with the posterior edge deflected inwards (Fig. 61B). Although no dorsal margin is preserved, its outline can be established from the area of overlap on the anocleithrum, where it appears to have been truncated to gently concave. Although no complete specimen is available, it is clear that the posterior edge is deeply embayed just dorsal to the region of the bend between the two parts of the bone. In lateral view, the ventral part tapers to an acute termination. The branchial lamina is small, hav-

ing maximum dimensions at the bend in the bone and tapering away dorsally. Ventrally it tapers abruptly, providing the articulation for the long dorsal process on the clavicle (Fig. 61B). Between this abrupt taper and the ventral tip of the bone, there is a narrow flange with a groove on its inner face into which the anterodorsal edge of the clavicle was loosely articulated.

According to Thomson & Rackoff (1974), the cleithrum of *Ectosteorhachis nitidus* consists of two separate bones. We can find no evidence of such a construction in *C. narrienense*, either from external or X-ray examination. In this respect *C. narrienense* resembles *Megalichthys hibberti*.

Over most of the external surface the sculpture consists of raised ridges making a strong tracery pattern. Distinct dorsal and ventral parts are obvious (Figs 60A; 61C). The dorsal part has one or two long straight ridges parallel with the anterior edge, posterior to which the ridges retain their height but become shorter and less regular, and carry tubercles along their crests (Fig. 60C,D); near the posterior edge, they become weaker and form a finer reticulate pattern. On the ventral part of the bone a similar arrangement occurs, except that the ridges become reticulate closer to the anterior edge. On the posterior angle of the bone and on the posterodorsal extremity, the ridges give place to small but distinct areas of cosmine (Figs 60A,E; 61C).

Clavicle. This bone (QMF26548, 26572) is only about half the size of the cleithrum. In its orientation it is twisted so that its main plane lies at about 40° to the plane of the upper part of the cleithrum (Figs 61B; 62C). It is thickest dorsally and thins out gradually towards the antero- and posteroventral edges. Its ventral edge is broadly rounded. A thick dorsal process extends up the inner edge of the branchial lamina of the cleithrum, from which it separates slightly towards its dorsal extremity. Ventrally, the branchial lamina tapers away about half way down the bone. On its inner posterior surface is a pronounced furrow into which the edge of the ventral extension of the cleithrum fits.

The external surface of the clavicle is covered with ridges of similar type to those of the cleithrum, but the pattern is different (Figs 60F; 61C). Long ridges border the anterodorsal edge but immediately behind, they are replaced by a reticulum. Anteroventrally the ridges are even lower and the reticulum finer, but posteroventrally a strip of unornamented bone is replaced by a patch of cosmine.

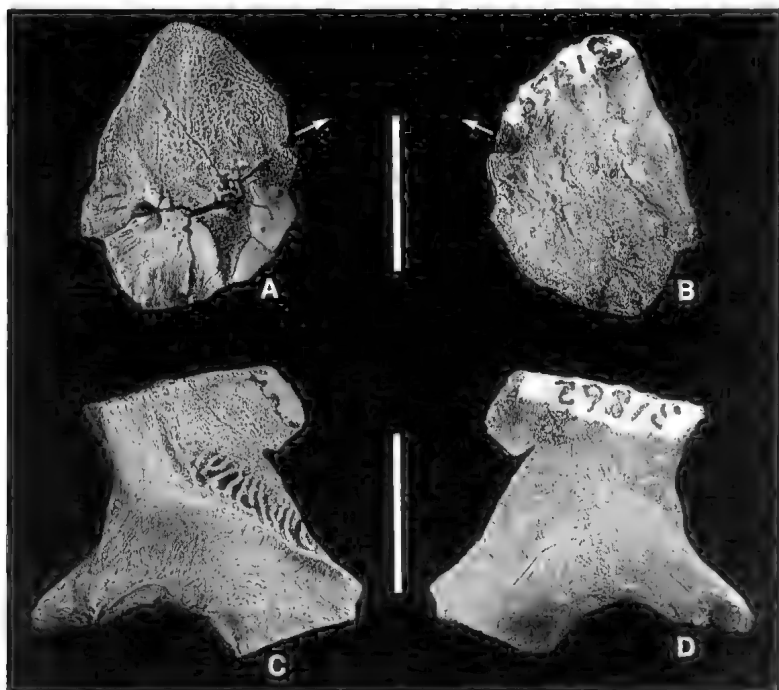


FIG. 59. *Cladarosymblema narrienense*. A,B, complete right supracleithrum, QMF31859, lateral and mesial views. Surface for the supratemporal overlap to the bottom left of the photograph in A. Arrows mark the entrance and exit points of the lateral line canal. C,D, incomplete anocleithrum, QMF31862, in lateral and mesial views. Both dorsal and ventral edges broken. Surface for overlap by cleithrum to the bottom left in C. Scale: 10mm.

The internal surface of the clavicle at its ventral edge has a large area showing that it overlapped another bone (Fig. 61A), which can only have been the interclavicle. We have not recognised any such bone in the etchings, probably because it would be rather nondescript and almost certainly broken. An interclavicle is recorded in *Eusthenopteron* and *Osteolepis*, but in each the overlap of the clavicle is small compared with that of *C. narrienense*.

Scapulocoracoid. This bone is known only from its areas of attachment to the cleithrum on QMF26548, and a crushed incomplete bone attached to QMF26554 (Figs 59A; 60B). It was a large and lightly ossified structure with three areas of attachment that are normal for osteolepiforms and Palaeozoic dipnoans (Andrews & Westoll, 1970a,b; Janvier, 1980). The attachments in *Cladarosymblema* are unusual, however, in their size and disposition. Anteriorly the scapulocoracoid is flattened on its mesial face and it apparently increases in depth rapidly as it approaches the fin attachment, which is not preserved. According to Jarvik (1980: 269) in

Glyptolepis groenlandica, which is a porolepiform, the scapulocoracoid is a small unperforated plate. Should this prove to be normal for that group, it would provide an excellent character for distinguishing it from the osteolepiforms.

The most posterior attachment ($ar^1Sc.$ cor. of Andrews & Westoll, 1970a: text-fig. 4), which lies in the posterior angle of the bone, is the smallest of the three, and is almost equidimensional (Figs 62; 63). Anteroventral to it is a much larger and more elongate attachment ($ar^3Sc.$ cor. of Andrews & Westoll), which tapers to an acute dorsal terminus. This attachment is for the infraglenoid buttress. The two are separated by a broad smooth surface which contained the subscapular fossa. The anteriormost attachment, which is for the supraglenoid buttress, is by far the largest. It extends dorsally along the anterior edge of the cleithrum in-

side the process on the clavicle and upwards on the inside of the branchial lamina; there it turns abruptly posteriorly towards the posteriormost scar ($ar^2Sc.$ cor. of Andrews & Westoll) to which it is joined by a low bridge of bone. This latter forms the floor of the supraglenoid foramen. The buttresses are so placed that the subscapular fossa is directed more anteroventrally and the scapulocoracoid foramen is directed more posteroventrally than the corresponding features in *Eusthenopteron* and in the unidentified specimen described by Janvier (1980).

The size of the scapulocoracoid and its attachment areas is greater than those of most other osteolepiforms. In this respect the species is similar to *M. hibberti* (see Andrews & Westoll, 1970b: text-fig. 2) and *E. nitidus* (see Thomson & Rackoff, 1974: pl. 2, fig. 1). As in these species also, the anteromesial face of the scapulocoracoid lies at a low angle to the blade of the cleithrum. The overall size of the bone correlates with the large basal part of the fin, which indicates the presence of unusually powerful musculature; the different orientations of the various fossae de-

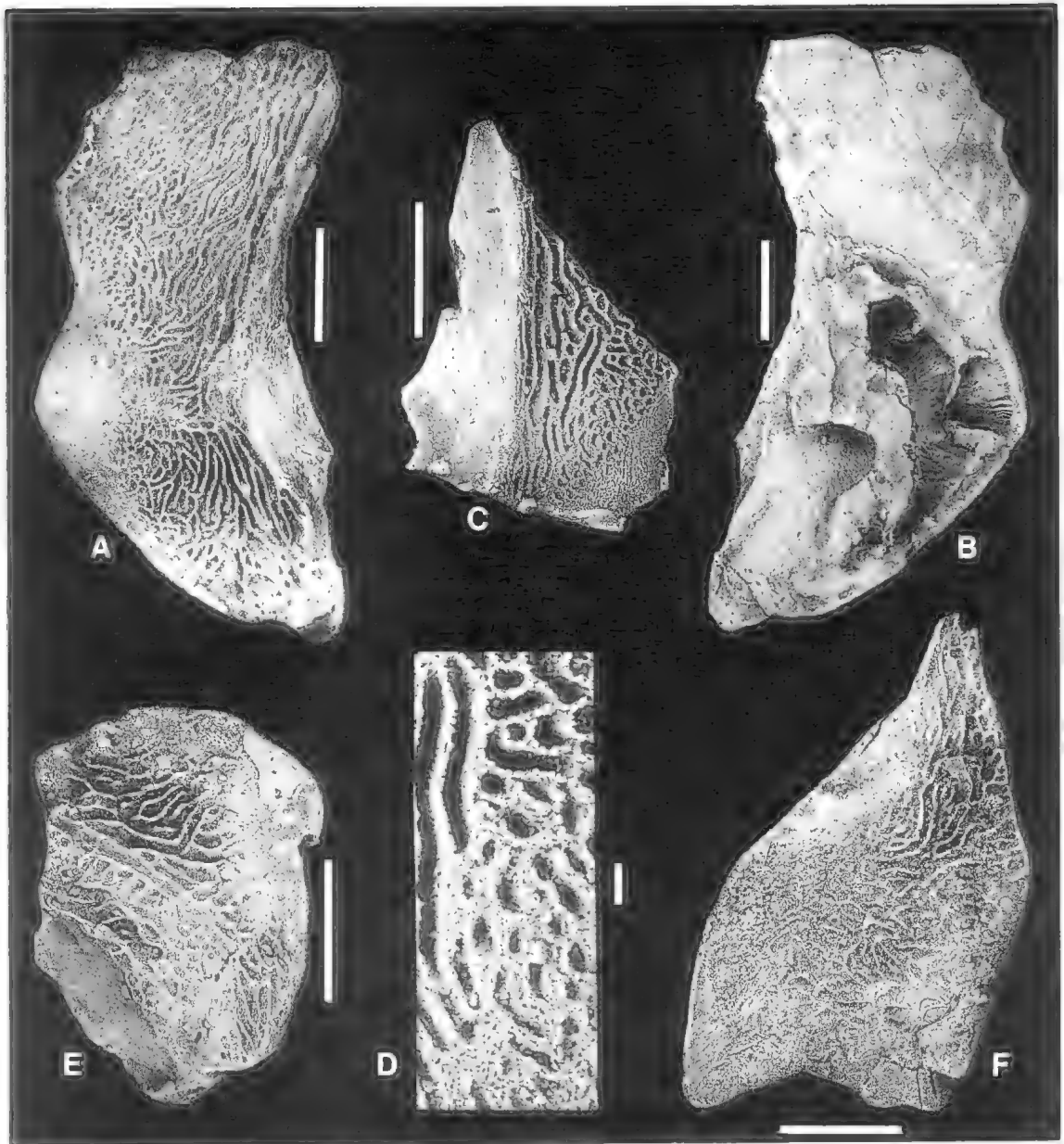


FIG. 60. *Cladarosymblema narrienense*. A,B, lateral and mesial views of an incomplete right cleithrum, QMF26554. B, showing large scapulocoracoid (see Fig. 63 for interpretation). C,D, part of incomplete cleithrum, QMF26563, showing the details of the ornamented surface. E, fragment of a left cleithrum, QMF31875, showing details of the surface ornament. Posterior extremity to top right of photograph. F, almost complete left clavicle, QMF26572. Dorsal edge to top of photograph. Scales: A-C, E-F, 10mm; D, 1mm.

scribed above, indicate that the fin muscles were differently oriented.

PECTORAL FINS

The pectoral fins are known only from the holotype in which the fin on each side has been

prepared to expose as much as possible of its surface. In comparison with most (but not all) other osteolepiforms they are large, the distance from the base to the tip being c.10cm in a fish whose head exclusive of the operculars is about the same length. The proximal 6.25cm is covered

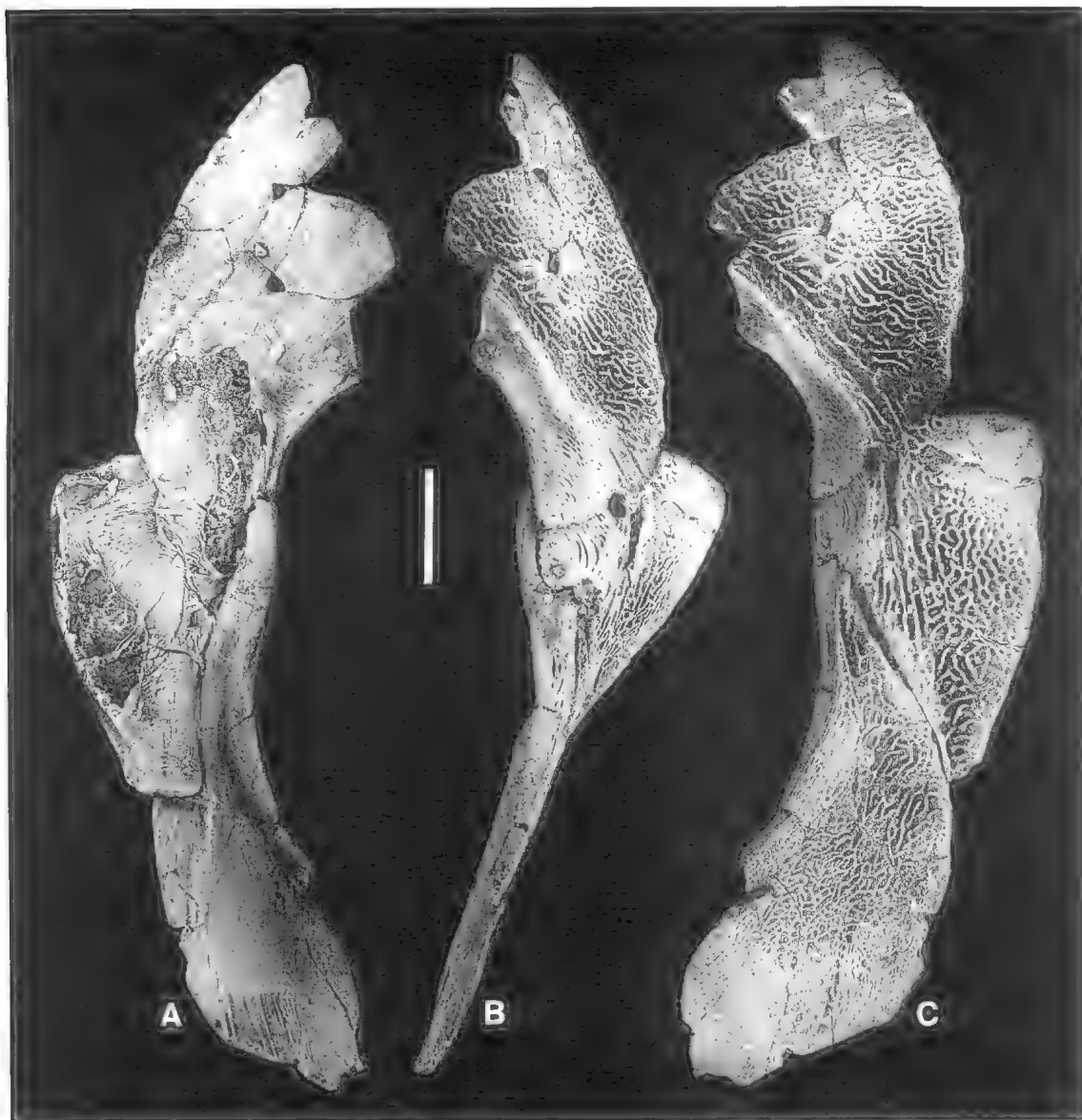


FIG. 61. *Cladarosymblema narrienense*. A-C, left pectoral girdle, QMF26548, A, mesial, B, anterior, and C, lateral views. (See Fig. 62 for interpretation.) Scale: 10mm.

with rhombic scales similar to those on the body (Fig. 64). They show a gradual decrease in size and become more elliptical in outline distally, the most distal scales being about one half as long as the proximal ones. The scales also change in shape towards the anterior edge of the fin, becoming similar to those at the distal tip about half way along the basal lobe (Andrews, 1973), whereas on the posterior side in equivalent positions, they are of the same size as the scales in the middle of the lobe. As noted above, one of the features of the

Osteolepiformes is said to be the presence of enlarged scutes on the edges of the basal lobes (Andrews, 1973), but we have not been able to recognise such on our specimen. This is probably an artefact of preservation. The ventral surface of the left fin has 60+ large scales.

Distally the scale size and shape abruptly change as the basal lobe passes into the ray scales. These ray scales are square or rectangular in outline (Fig. 64C). At mid-fin, the proximal ray scales are square and average 0.75mm in length.

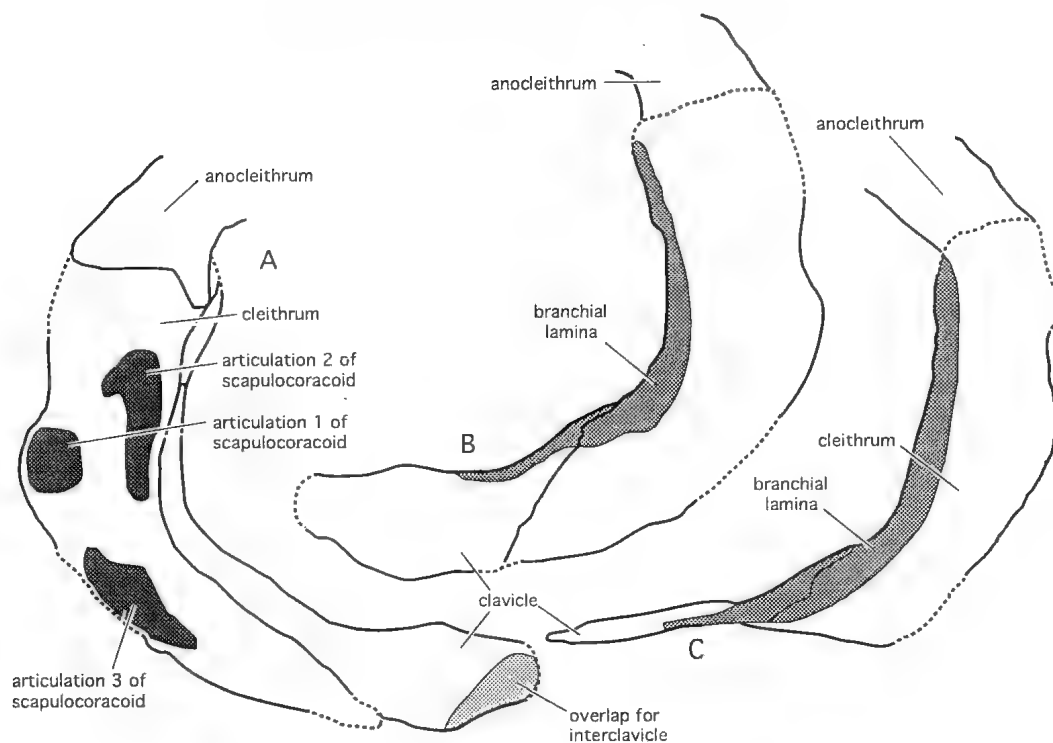


FIG. 62. *Cladarosymblema narrienense*. Outline restoration of the shoulder girdle based on the specimens shown in Figs 59-61. A, mesial, B, lateral and C, anterior views.

They increase slightly in size to a point about 0.6-0.7cm from the end of the basal lobe, where they abruptly divide into two rays. Further division takes place distally. Still further distally the scales become narrower and more elongate, ranging in length from 0.5-0.75mm and in width from 0.4-0.8mm. On the anterior of the left fin, the proximal fin ray scales are more elongate, measuring as much as 2.5 x 1.0mm. At mid-length of the dermal rays, the left fin has 120+ rays on its ventral surface.

An important feature of the ray scales is that they are all laterally contiguous; there is no evidence that they were able to separate to form an expanding surface with intervening membranes occupying a significant part of the fin surface. Another line of evidence suggests that expansion of the rays was not possible. The fins of *Latimeria* and such fossil sarcopterygians as *Eusthenopteron* have a limited number of long rays extending from only a small part of the basal lobe. In *Eusthenopteron*, about 80-100 long rays extend mainly from the distal part of the fin lobe, where

they could separate unimpeded by the shorter rays originating from the anterior and posterior edges of the lobe. Hence, if each ray was separated by only 1° from its neighbour, the fin fan could be expanded by up to 80-100°. In *Cladarosymblema* the rays are distributed much more evenly around the fin lobe, and there is no abrupt break in their length on either the anterior or the posterior edge. As a result, there is little space for an expansion of even 1° to take place between adjacent rays.

The basal lobe is clearly defined along its posterior edge where quite large scales give way abruptly to the fine dermal ray scales (Fig. 64C), but on the anterior edge the junction between the two types of scales is much less abrupt, some evidence of interdigitation being observed on the left fin. Unfortunately the anterior edge of neither fin is completely preserved.

An attempt has been made to excavate the axial skeleton of the left fin, but without success. The preservation of the whole structure is such that it

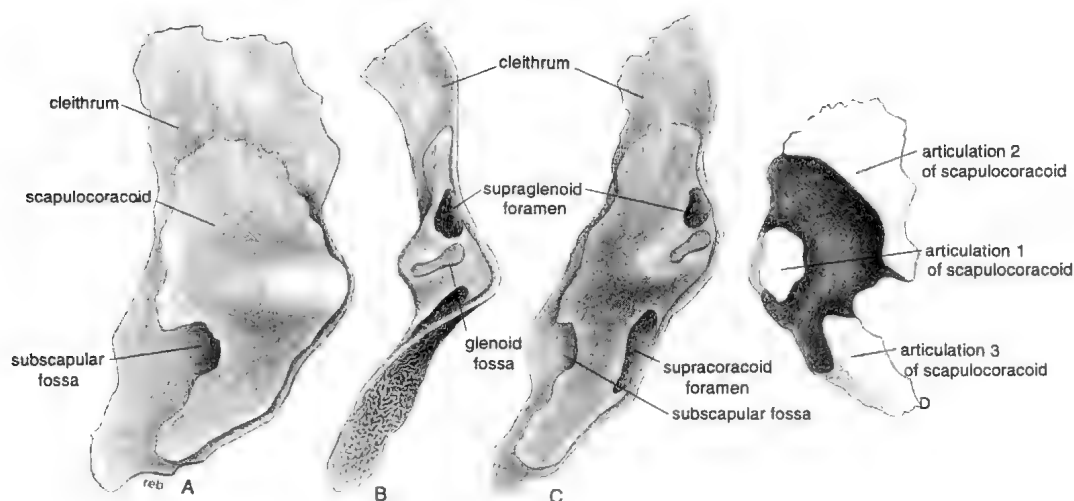


FIG. 63. *Cladarosymblema narrienense*. Restoration of the scapulocoracoid based on the specimens in Figs 60B and 61A. The restoration lacks control on the shape and size of the posterior part of the scapulocoracoid, and the size and shape of the glenoid fossa which may be too small judging from the reconstruction of *M. hiberni* by Andrews & Westoll, 1970b. All views, except D, with scapulocoracoid still attached to the coracoid. A, mesial, B, posterior, C, posteromesial and D, internal view of the scapulocoracoid after removal from the

would have been found if it were present. We can only conclude that it was poorly ossified.

AXIAL SKELETON

Ring centra appear infrequently in the etchings, no doubt because of their fragility. The best preserved one is from the trunk and is 4.2mm long, 16.0mm in diameter, and 11.5mm in notochordal diameter (Fig. 64D,E). These proportions are approximately the same as those of a much larger specimen of *Megalichthys hiberni* figured by Andrews & Westoll (1970b: pl. 3, fig. H), although the bone tissue in our material is somewhat thinner. The preservation is adequate, but removing all the sediment from the surface has proved impossible. Ventrally there is a slight flattening marking the position of the dorsal aorta. Its anterior and posterior faces are approximately parallel up to the points where the neural arch was articulated; at those points it is obliquely truncated and the ring is not complete. As indicated by Andrews & Westoll (1970b: 421), although many centra of *M. hiberni* are complete annuli, some trunk centra have a gap dorsally, like the present specimen. Comparison should be made also with the figures of *Ectosteorhachis*

nitidus presented by Thomson & Vaughn (1968: figs 1 & 2).

The outer surface of the ring is largely, or perhaps completely covered with periosteal bone, within which an anterior and a posterior groove can be distinguished laterally. The deeper groove is on what is considered to be the posterior side, based on the shape of the facet for the articulation of the neural arch. These grooves presumably mark the position of the myoseptum and the inter-segmental artery. No semblance of a distinction between intercentrum and pleurocentrum is present.

We also have recovered one or two poorly preserved neural arches that possibly belong to this taxon but are not worth figuring or describing.

SCALES.

Gross Morphology. Numerous isolated scales are available for study in addition to those on the holotype. Although their outlines vary greatly according to their position on the body, the exposed cosmine-covered part is almost always rhombic in outline, with the long axis of the rhombs oriented approximately along the length of the fish (Figs 5; 6). As would be expected, the rhombs tend to be symmetrical in scales from the mid-line and the mid-flanks (Fig. 65B), but asym-

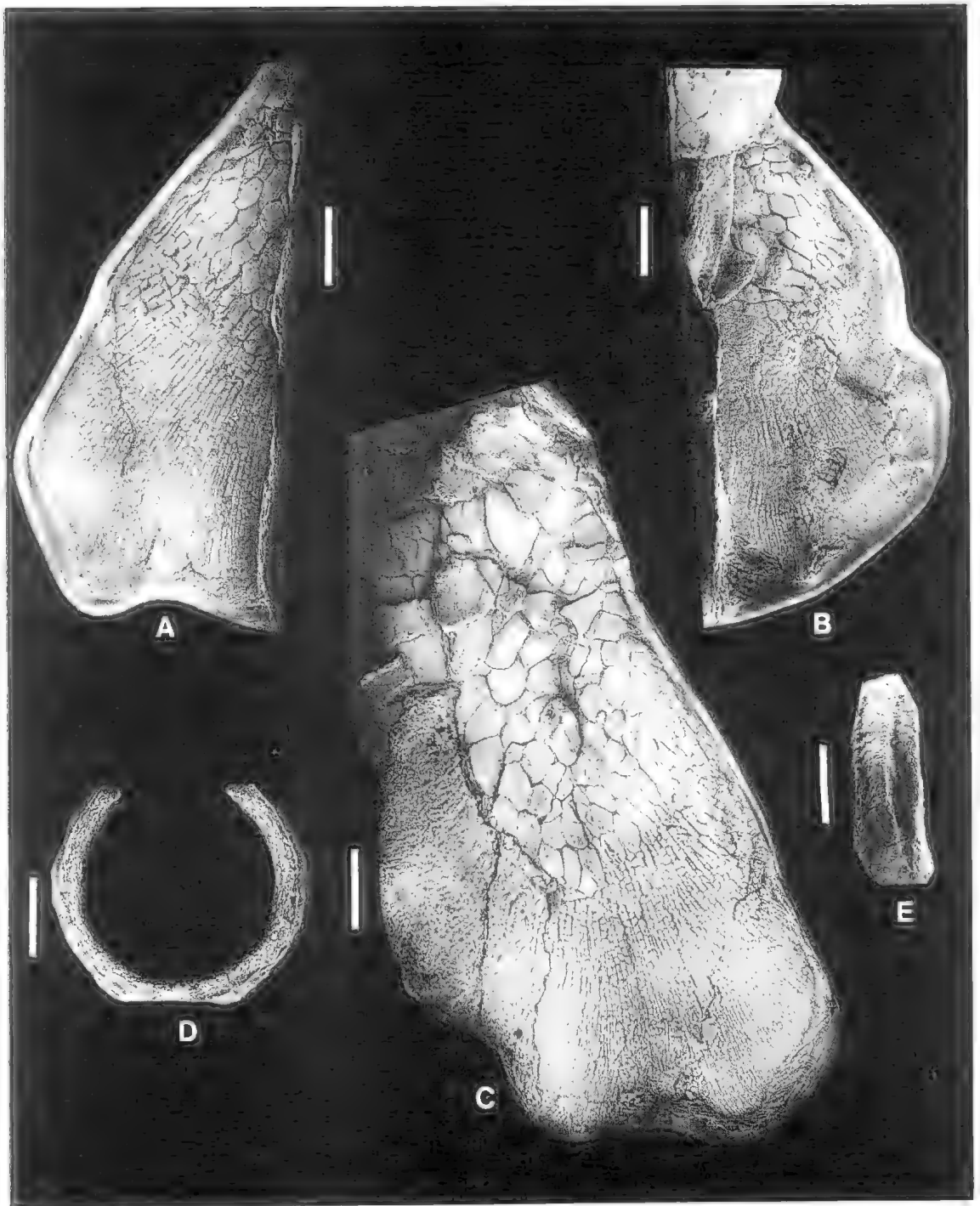


FIG. 64. *Cladrosymblema narrienense*. A, B, left and right pectoral fins of holotype (QMF21082) in dorsal view. Inner margins of fins are obscured by the overlying body of the animal. C, ventral view of left pectoral fin. (Note that edges of both fins are bordered by reinforcing wires used during preparation). (See Figs 5 and 6 for a more general perspective.) D, E, anterior and left lateral views of an isolated ring centrum, QMF31881. Scale: 10mm.

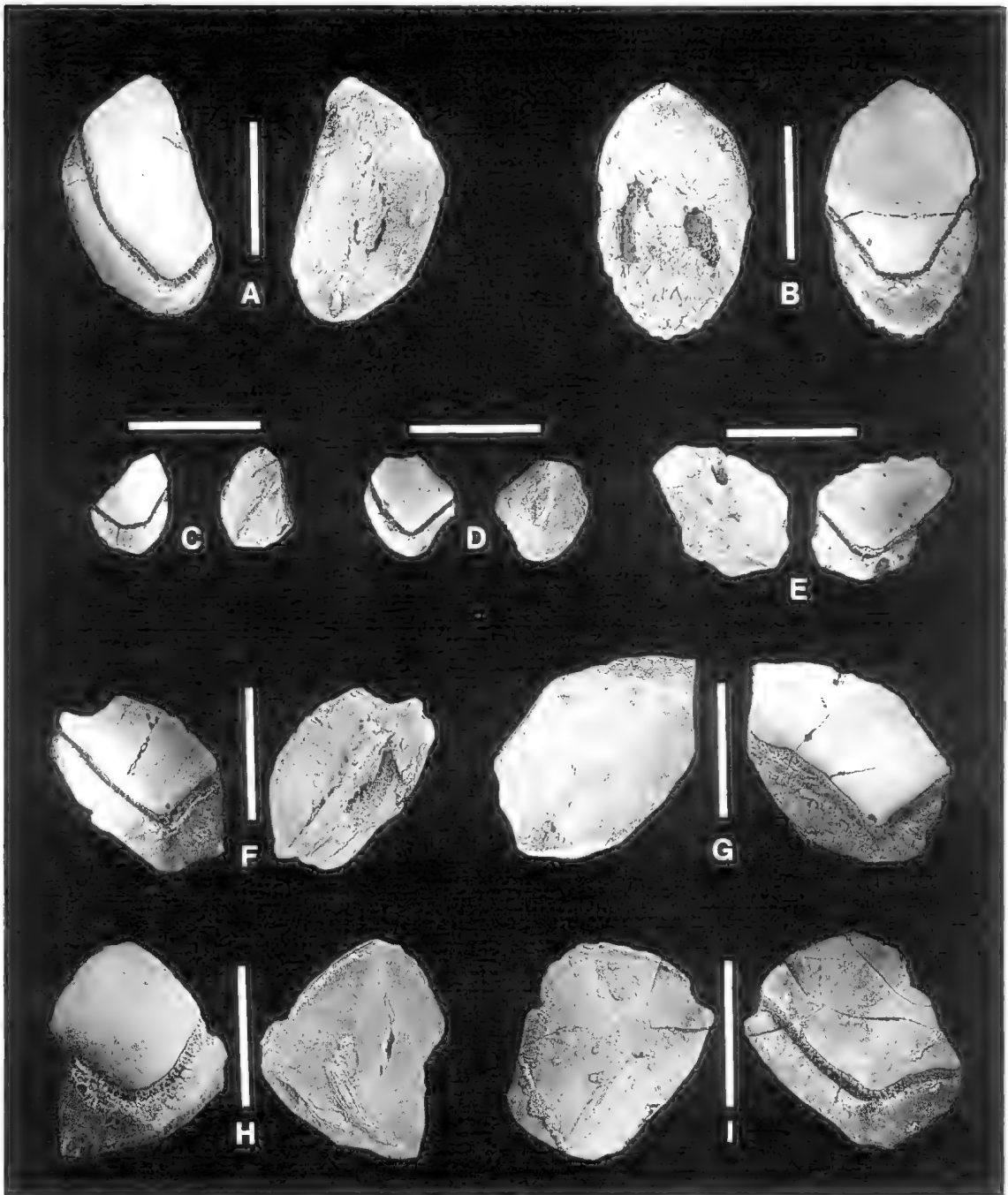


FIG. 65. *Cladrosymblema narrienense*. Scales from different parts of the body in external and internal views. Scales are almost complete. A, from left lower flank, QMF31889. B, from mid-flank, QMF31881. C,D, small scales from mid-line, QMF31891-2. E, lateral line scale from flank, with openings for canal shown, QMF31893. F, from right dorsolateral flank; posterior edge broken, QMF31894. G, overlap on left side of photograph turned down sharply, implying a position adjacent to a sharp change in body conformation, QMF31895. H,I, flat scales from anterodorsal or anteroventral body, QMF31896-7. Note variation in the nature of the ridges and irregularities on the inner surfaces. Exposed vascular bone in the gutter bordering the cosmine surface is well shown in A, G, H and I. Scale: 10mm.

metrical in those dorso- and ventrolaterally situated on the body. Symmetrically arched scales, assumed to be from posterior mid-dorsal positions, are included in our sample (Fig. 65C,D).

The rhombic part of a flank scale occupies about two-thirds of the surface area of the scale. It is separated from the overlapped bony surface by a strong groove or gutter which exposes coarse vesicular bone (Figs 65F-I; 66A). The remainder of the overlapped surface is usually covered with dense lamellar bone on both inner and outer surfaces. This overlapped part is usually in the plane of the remainder of the scale, but occasional individuals, which must have come from parts of the body where the curvature was high, show the overlap intumed at an angle (Fig. 65G).

The scales never have a peg and socket structure; they apparently depended entirely on overlap and soft tissue to maintain their position on the body. The inner surface of some scales has a strong ridge that could be interpreted as the remnant of an original peg and socket ridge. This ridge is very variable in form and orientation, ranging from narrow and sharp-keeled to broad and flattened. Normally, the ridge shows a series

of striations parallel with its length, these indicating the addition of successive layers of bone independently of the layers forming the remainder of the internal surface (Fig. 65F,H,I). In addition its margins are commonly undercut, suggesting either resorption or the failure of the collagen-rich isopedin to mineralise (see below) (Figs 65F; 68C). It should be noted that the ridge is absent, or only poorly developed, on many scales.

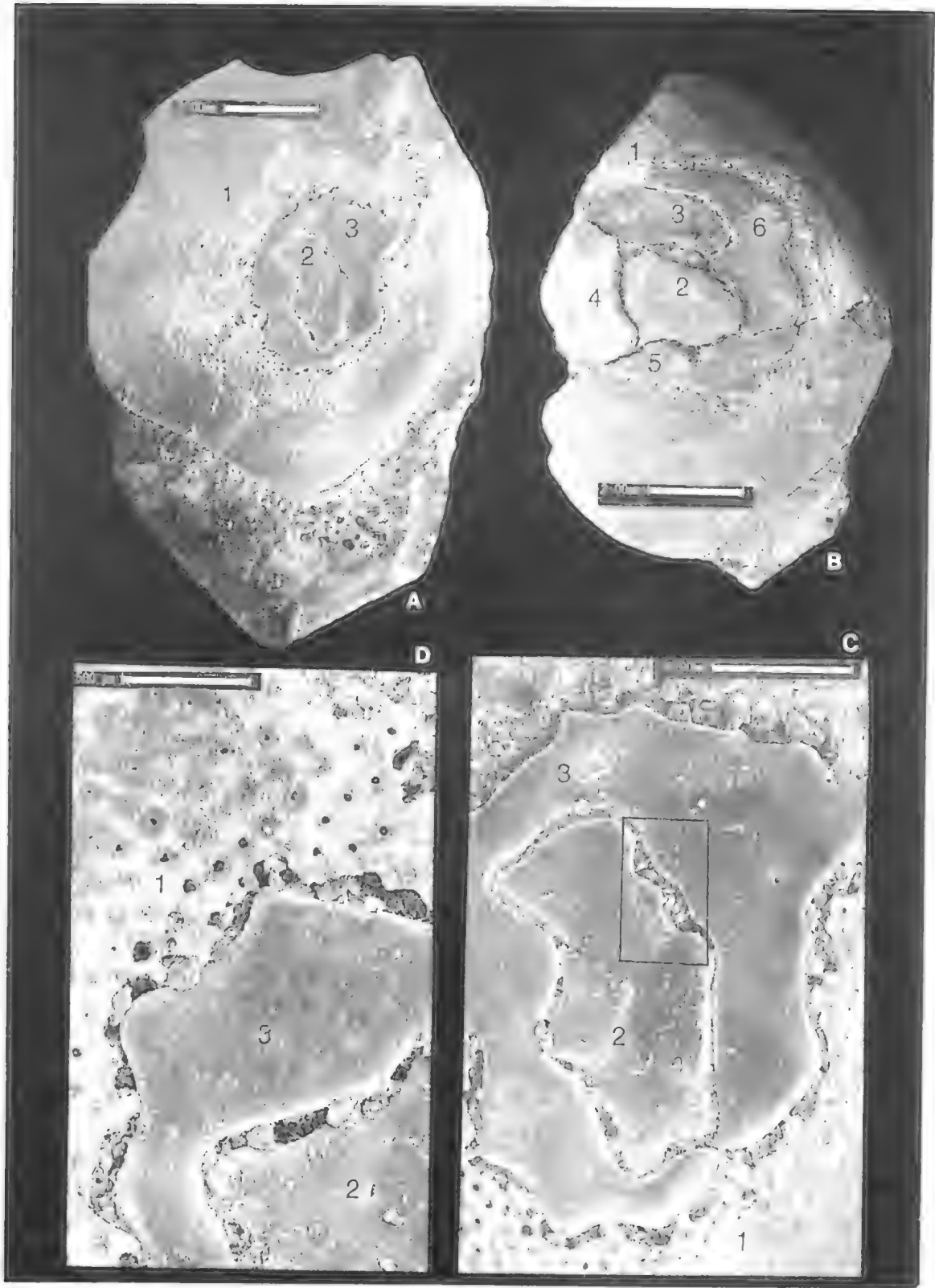
As well as the ridge, several other features of the internal surface are noteworthy. Many scales are not smooth but show a variety of apparent resorption features, from an extreme in which almost the entire lamellar layer is missing and the vesicular layer is exposed, to a condition in which a number of irregular mounds are scattered over the surface, to one in which only a few small depressions separate broader flat surfaces (Fig. 65B). In addition, it is not uncommon to find a scale in which one or more of the lamellar layers is only loosely attached to other inner layers. As indicated above, we take this to mean that mineralisation of the collagen-rich isopedin layers was incomplete when the animal died, allow-

facing page

FIG. 66. *Cladarosymblema narrienense*. A,B, SEMs of two incomplete scales showing resorption and new cosmine growth. A, shows removal of the enamel layer in a broad band around the resorption ring, exposing the tops of the enlarged flasks, QMF31902. Near the bottom of the scale (arrow) only part of the enamel has been removed. B, a similar scale, QMF31903, with a central patch of replacement cosmine (2), and an incomplete annulus of replacement cosmine which is composed of four incomplete segments, (3-6). Note that at the time of death, parts of the margins of 3 and 4 were in process of resorption, and all the margins of 5 and 6 were in process of growth, indicating they may have been part of the same growth phase. C, enlargement of central part of A. In the centre of the resorption patch is regrown cosmine in process of resorption again. Note that in places its margins are entire, but at the points marked (arrows) they are irregular. An enlargement of the area (rectangle) is shown in Fig. 70A. These two scales demonstrate that cosmine replacement is a multiphase phenomenon. D, shows an enlargement of the bottom left of C in a rotated orientation. Note the resorption edge in the old cosmine is highly irregular and in places seems to have been progressing without the coalescence of enlarged pores. Note also dark rings around the pores in both the old and the new cosmine. The specimen was gold-coated, and hence these rings represent slight depressions in the surface. We consider that the depressions are the result of slight *post mortem* shrinkage around the flasks after the decay of soft tissues in the flasks. Those in the old cosmine may be emphasised because the underlying dentine around the walls of the flasks has been resorbed. In all figures, 1 denotes the oldest, and subsequent numbers, successively younger phases of cosmine growth.

overleaf on p. 192

FIG. 67. A-D, *Cladarosymblema narrienense*. All SEMs. A,B, central part of a scale, QMF33055, at two magnifications. In A note the unchanged pores at the top of the photograph, the progressive increase in size downwards as the enamel becomes thinner, and finally the area of complete resorption around the newly formed cosmine towards the bottom of the photograph. B, enlargement of part of A to show the finished edge of the new cosmine and the details of the resorption edges above. C, part of the surface of a large scale, QMF31904, showing new cosmine occupying almost all available resorbed space. Old cosmine adjacent to the resorbed edge shows no evidence of enlarged flask chamber openings. New cosmine stands a little higher than the surrounding old surface, forming low blisters. Scale: 1mm. D, surface of a scale on which resorption has just begun. Unlike the previous figure in which no enlargement of the pores has taken place, and Figs 66A,B and 67A,B in which the walls of the flasks have been resorbed in an irregular fashion, the more deeply resorbed pores in this figure show regular walls down as far as the mesh canals. Cosmine phases numbered as in Fig. 66.



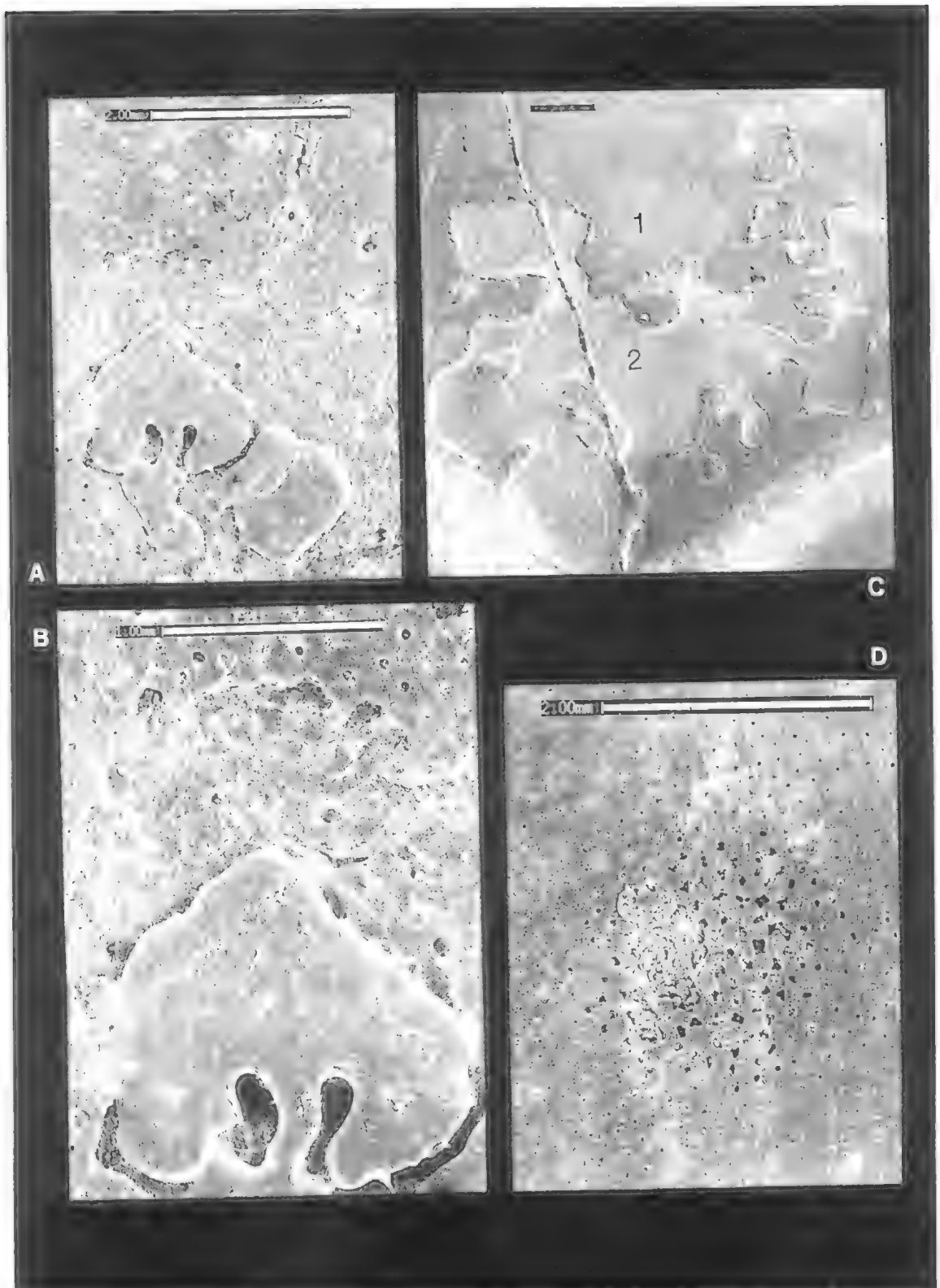


FIG. 67

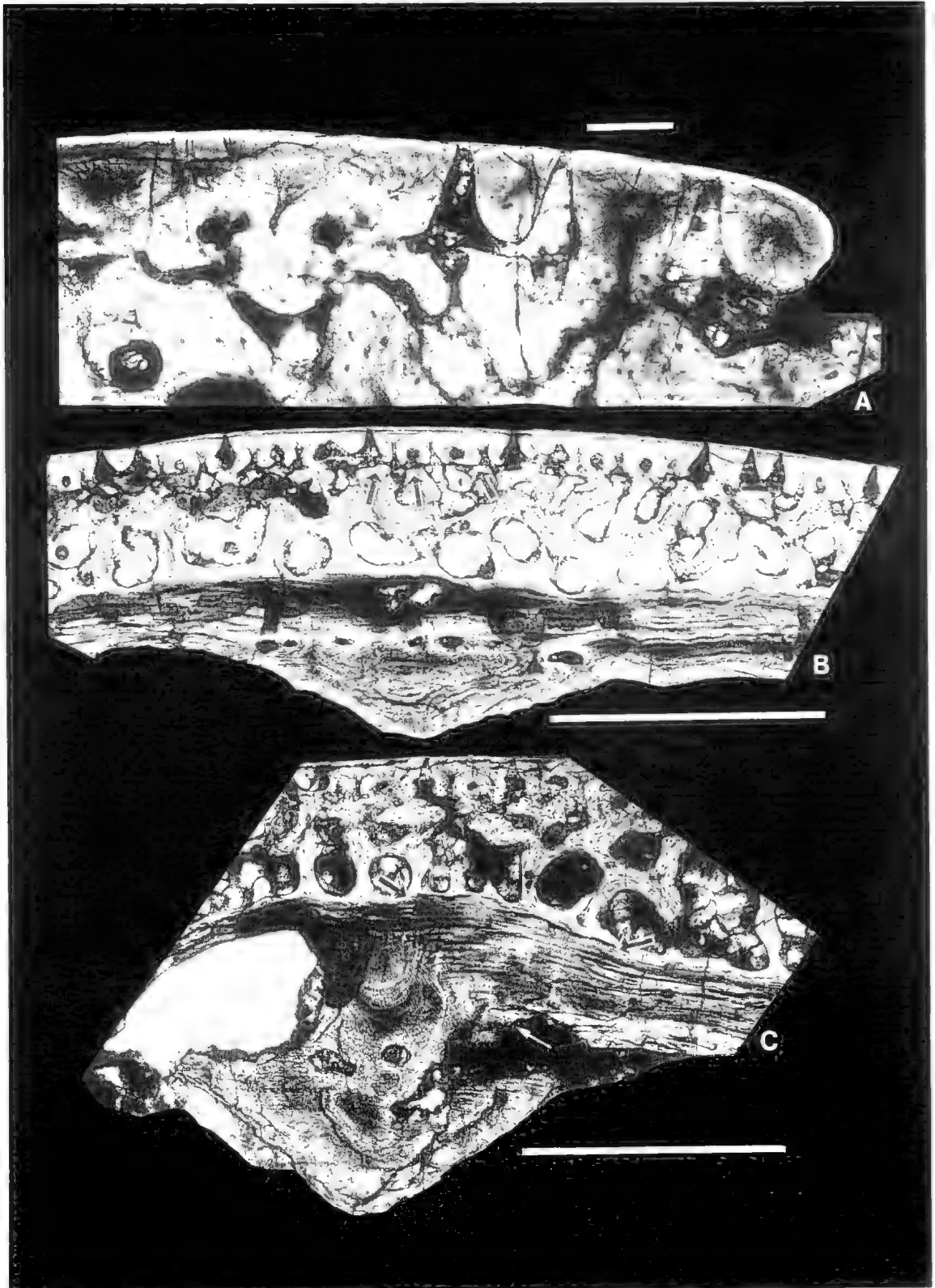
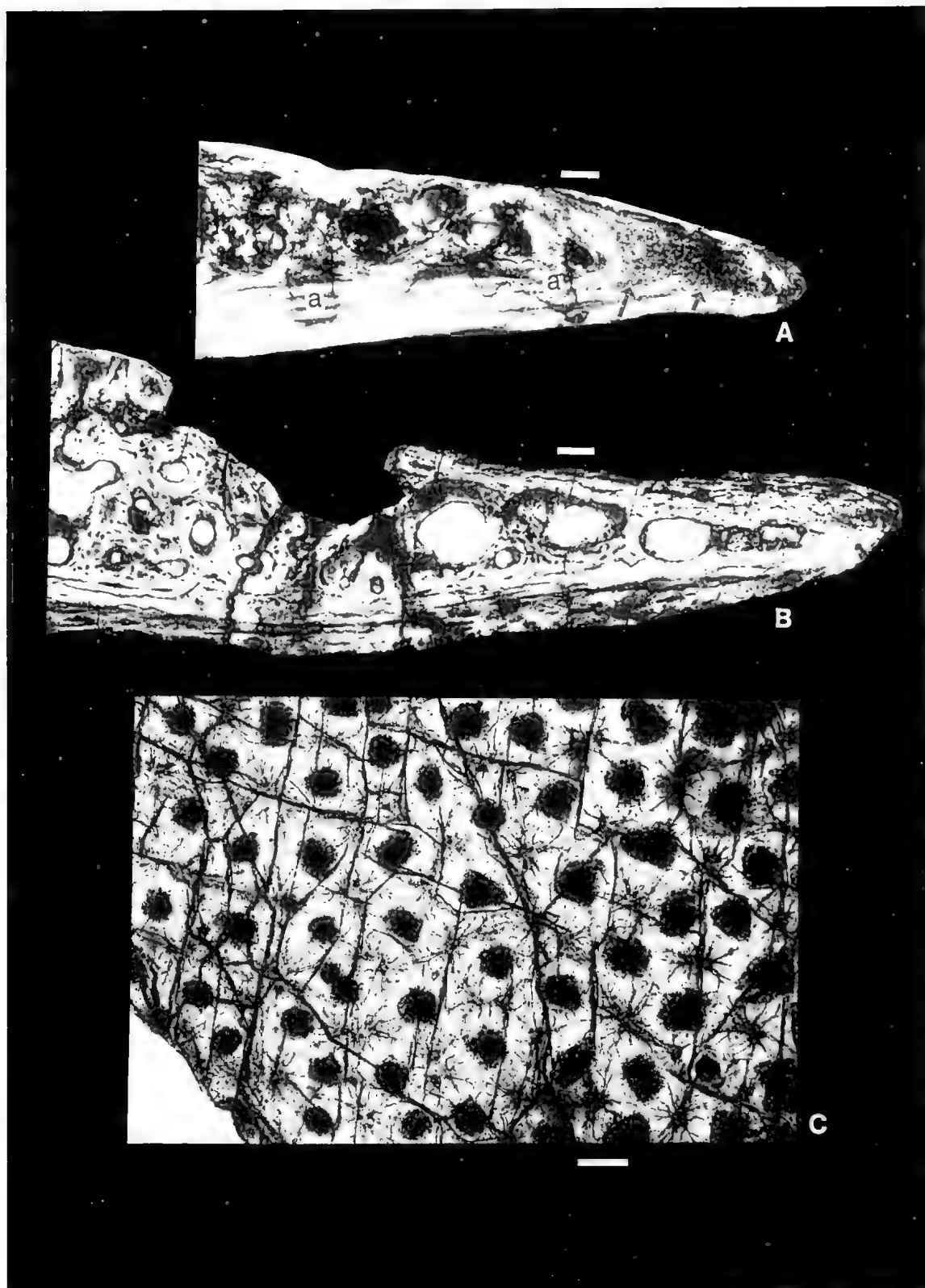


FIG. 68



ing separation of the ossified layers to take place after the collagen decomposed. As Kerr (1955) has shown for extant dipnoans, and Smith et al. (1972) have shown for *Latimeria*, the lamellar isopedin is composed mainly of collagen fibres, some of which become mineralised. In Devonian and Carboniferous dipnoans the mineralisation of these lamellae has proceeded almost to completion (Pridmore & Barwick, 1993). This then raises the question of whether the above-mentioned patchy appearance is the result of resorption or incomplete mineralisation. We have reached the conclusion that resorption is at least a partial cause. Thin sections show that the internal ridge is often bounded by gaps in the lamellae, but in some sections, the ridge lamellae terminate sharply against the truncated ends of other lamellae (Fig. 68C: black arrows). This has the appearance of resorption prior to the growth of the ridge.

The lateral line has been observed on isolated scales (Fig. 65E). It enters the scale anteriorly in front of the deep groove, and exits it posteriorly on the inner surface well anterior to the edge of the scale. Thus the line is completely covered from the exterior, and opens to the surface only through a number of large pores. A dorsoventrally oriented thin pit-line is visible on some scales.

The preservation of the holotype does not allow an exact count of scale rows, but we estimate that

there were c.15 vertical rows on each side of the trunk between the pectoral fin and the broken end of the specimen.

We have not recognised Westoll lines on any of the cosmine, but irregular resorption patches enclosing some regrowth have been observed. An occasional specimen shows resorption lines subparallel with the edge of the cosmine (Fig. 66A,B); however, most patches do not show any pattern with respect to either position on the scale or shape (Fig. 67C). As a result, our material supports previous studies (Westoll, 1936; Borgen, 1989, 1992), which have concluded that resorption is not normally, if ever, related to marginal growth of the cosmine. Those resorbed patches that are within the cosmine area are unevenly distributed, and the replacement cosmine was obviously expanding rapidly to fill the vacated spaces at the time of death. This new tissue was sometimes at the same level as the surrounding surface, and sometimes slightly raised to form a low blister.

A common phenomenon in the scales of *Cladarosymblema* is the resorption of the superficial layer of enamel in a wide band around a resorption zone that cuts through the whole cosmine layer (Fig. 66A). This is taken to represent the first stage of cosmine resorption. Subsequent to the removal of the enamel, but in advance of the deep resorption edge (Fig. 66A-D), the size of

overleaf on p. 193

FIG. 68. *Cladarosymblema narrienense*. Thin sections of scales showing internal structures. A, section, QMF31900, showing the edge of the cosmine with the enamel layer wrapped around the end of the dentine. Three flask chambers open vertically into the bone vesicles, the osteocyte spaces being conspicuous. The dentine 'trees' are well developed. B, part of vertical section, QMF31899, through the whole thickness of a scale including the ridge on the inner surface. Note the clearly defined cosmine layer and the cross-canals in the centre of the photograph (arrows) showing greater regularity than normal. The inner lamellar layer is thickened at the median ridge which shows some lamellae folded back on themselves, indicating that the ridge was not formed simply by thickening of the lamellae. C, vertical section, QMF3898, of a scale to show the structure of a ridge in detail. Note resorption on the right (white arrow), some continuous lamellae between the ridge and the vesicular bone, the interrupted lamellae immediately under the vesicular bone (black arrows), and the irregular, almost chaotic arrangement of the tissue forming the bulk of the ridge. Scale: 1mm.

facing page

FIG. 69. *Cladarosymblema narrienense*. A,B, two vertical sections through the overlapped parts of two scales. A, QMF31899, basal lamellar layers are progressively truncated against the vesicular layer, and towards the right extremity, note the breakdown of the lamellae (arrows) immediately prior to resorption and replacement by vesicular bone. Irregular patches (a) are gas bubbles in the slide. B, QMF31900, section cuts across edge of the cosmine and its surrounding gutter, exposing the vesicular layer. Note basal lamellae truncated against the vesicular layer, but outermost ones continue around the scale margin on to the outer surface. C, QMF31901, horizontal section through the dentine layer of the cosmine of a scale, cut near the level of the top of the pulp canals, QMF31901. Large black openings are flask chambers and radial arrays of the dentine tubules are obvious. Note that the tubules are bent so that they are approximately radially arranged around the flasks as well as the pulp canals. Contrast this with the organisation in the unidentified osteolepidid scale figured by Gross (1956: pl.10, fig. 3). Scale: 0.1mm.

the flask-chamber pores is enlarged in a systematic fashion, indicating that scleroclasts occurred within the flask chambers, as Borgen (1989, 1992) has argued. However, in our material the resorbing edge is not formed from coalescing enlarged flasks, but rather from the junction between an advancing front of resorption and the resorbing margins of the flasks. This evidence indicates that scleroclasts were present in the bone and that some of them migrated into the flasks in advance of the resorbing front. This view is confirmed by examination of Figs 66D & 70A, in which a zone of resorption is bordered on one side by an advancing edge, and on the other by a ragged edge of resorbed cosmine. The latter shows no sign of enlarged cosmine pores, indicating that resorption took place by an advancing front alone. In addition, Fig. 67C shows a scale in which there is no evidence of enlarged flask openings in advance of the resorbing front. We conclude from this that the function of the flask chambers could not have been *only* to house the cells involved in cosmine removal, although such cells did function from the flasks in at least some specimens during resorption phases. As Borgen has pointed out, the soft tissues on the surface of the scale could have been supplied with nutrients only via the flasks, and presumably this must have been a second function. The degree of organisation of the flasks and the cross canals, however, is far in excess of what would be necessary to serve these two functions.

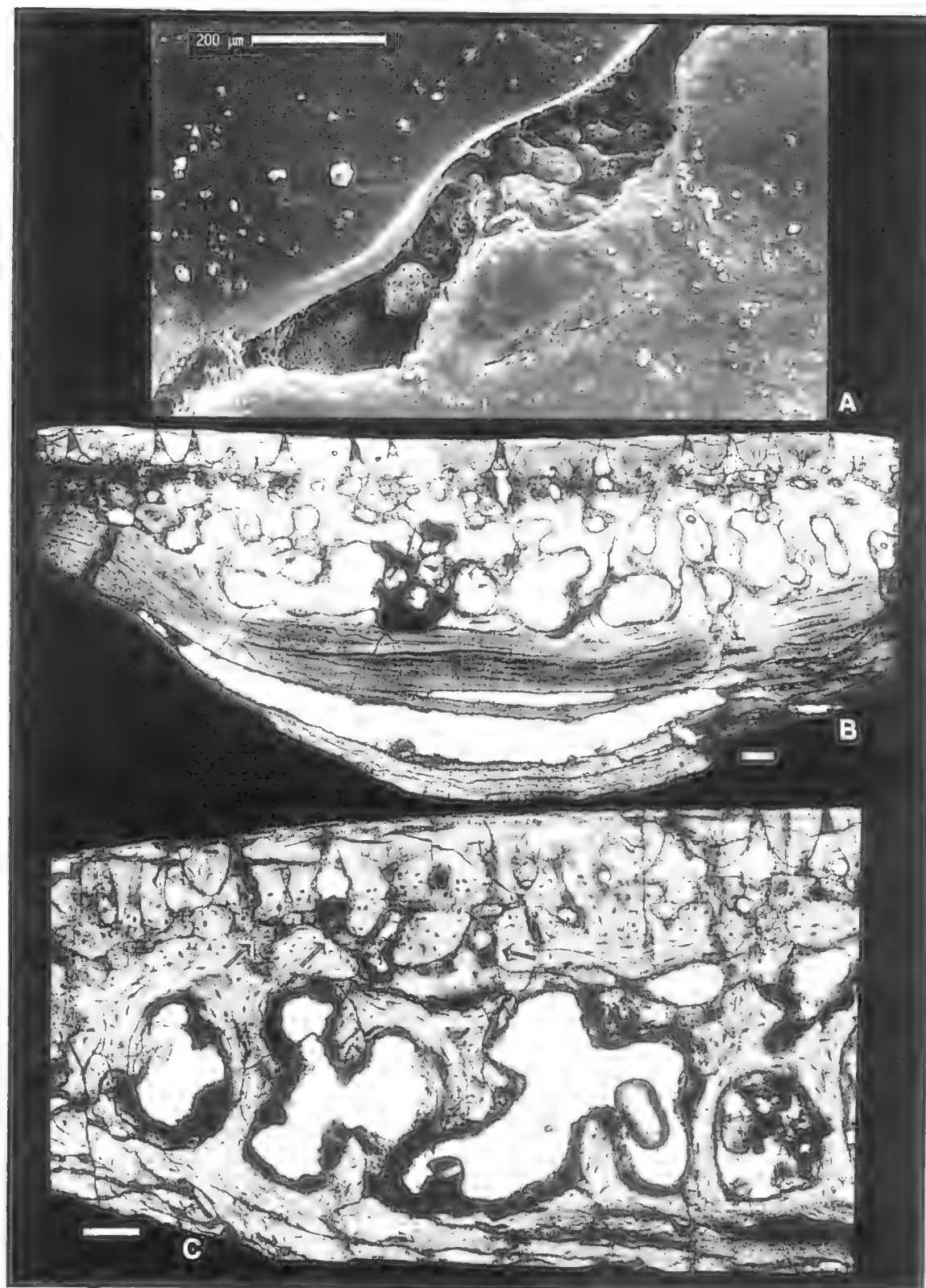
Scale Histology. Sections of the scales are shown in Figs. 68-74. The enamel layer (or enameloid according to Meinke & Thomson, 1983) is thin and overlies a thick dentine layer in which the cosmine flask chambers lie. The enamel layer folds over around the finished edges of the cosmine as shown in Fig. 68A, but as that section shows, no downturned enamel edges are seen buried within the cosmine. This means that at least the margins of the cosmine would have had to be resorbed to allow growth (Gross, 1956; Thomson, 1975). The matter is discussed below under Scale Growth.

The flasks are very fine, and their openings to the surface are only 7 - 10 microns in diameter.

They are closely spaced, the count being c.60 per square mm. In vertical thin sections the upper parts of the flasks are almost conical in shape or have concave walls, there being little outward curvature of the walls to produce pear shapes (Figs 68A,B; 70B,C). In horizontal section, the flasks show irregularities in the lower half of the chambers because of folding to produce the mesh canals (Figs 71A; 72A). These mesh canals are highly variable in shape (Figs 68A,B; 70B,C; 71A,B). Some have their greatest diameter where they join the flasks, but decrease dramatically to less than half that value where they interconnect with those from adjacent flasks. In this respect the mesh canals are very similar to those figured for *Megalichthys laticeps* by Gross (1956: fig. 51), but unlike those figured by Thomson (1975: figs. 26-28) for *Ectosteorhachis nitidus*. On the other hand, some scales have flasks and thin mesh canals closely comparable with the latter. Nor are the canals regular in number. Some chambers have three and others four mesh canals joining their bases, in some areas three dominating and in others, four. An occasional flask shows five mesh canals. The arrangement depends on the packing arrangement of the flask chambers. The mesh canals are always on one level rather than two, as Gross (1956: figs 34A,B) figured for certain osteolepiforms from Estonia. In those specimens he recorded 'Unter-Maschkanalen' as well as 'Maschkanalen'.

At their bases the flasks extend into vertical canals, some of which are so broad that they occupy almost the whole width of the base of the chamber (Figs 68A,B; 70B,C; 73B). These are joined laterally in an irregular fashion by branches to the vertical canals of adjacent flasks and to the pulp canals to form the cross-canals (Gross, 1956; Thomson, 1975). Although their arrangement is much less regular than in *M. laticeps*, these are very roughly sub-radially organised around the pulp canals, and only incidentally join the bases of the flasks. As can be seen from Gross (1956: figs 48A; 50C) the diameter and arrangement of these canals is very variable in *M. hibberti*, and some of them, instead of joining into the base of an adjacent flask chamber,

FIG. 70. *Cladarosymblema narrienense*. A, SEM of part of scale, QMF31902, in Fig. 66C, to show partial resorption of the second generation of cosmine (bottom right) and the advancing third generation (top left). B,C, two vertical sections through a scale. B shows well-preserved tissue layers and flask chambers, QMF31900. Basal lamellae show gaps that are the result either of separation during preservation, or failure to mineralize layers of collagen. C, section QMF31898, has the lamellar layer disrupted, but shows the flask chambers opening down into irregular cross-canals (arrows) and the relationship between bone containing osteocyte spaces, bases of flasks, and pulp canals. Scales B-C: 0.1mm.



turn down into the vesicular bone. Many of them do the same in *C. narrienense*.

Each dentine column between adjacent flasks is almost invariably organised around a single pulp canal that terminates in very variably arranged tubules (Figs 68A,B; 69C; 70C; 71A,B). Occasionally two closely-spaced pulp canals are present between a group of flask chambers (see right end of Fig. 70B and the region to the right of centre in Fig. 69C). The tissue flanking the flask chambers above the level of the mesh canals is dentine, whereas the deeper tissue around the vertical and cross-canals contains osteocyte spaces (Figs 68A; 70C), some of which have arachnoid shapes like those figured by Thomson (1975) for *E. nitidus*. The space between the vertically standing cylinders was filled with dentine deposited from and between the variously oriented branched ends of the tubules. From the outer ends of the pulp canals, branches radiate in the usual way (Fig. 69C), and these give rise to dentine tubules that are easily visible, many being stained by iron compounds. In vertical section the vertical pulp canal itself is often *apparently* devoid of surrounding tubules, although the tubules can be distinguished at high magnifications with appropriate illumination. On the other hand, horizontal sections show that dentine canals ramify from the trunk in much the same way as at the top of the pulp canals (Figs 69C; 75C). The reason for this apparent discrepancy is the fact that it is unusual for a vertical section to intersect one or more of the main lateral trunks from the canal, and only the intersections with the more numerous fine tubules are seen.

The dentine shows distinctive patterns in thin section. The crystallites forming on the flanks of the flask chambers are disposed normally to the surfaces of the flasks. This is inevitable because the first-formed layers of mineralisation were deposited around the flasks, as they indeed have to be because the flasks, which open to the exterior, must have been present when the first dentine tissue formed. Subsequently, mineralisation retreated towards the pulp canals. However, although in thin section it is difficult to see growth lines of the kind illustrated by Thomson (1975: fig. 21) around the flask chambers of *E. nitidus*, they can be readily recognised in SEMs of etched surfaces (Fig. 71A,B). We have illustrated such growth lines in Fig. 75.

There is optical continuity in the crystallites surrounding each flask chamber, and under crossed polars the extinction cross moves as though it formed a unit with the optic c-axes of

the crystallites radially arranged. For obvious reasons, the crystallites must have a radial disposition around the pulp canals as well as the flask chambers. Because the dentine tubules are also disposed normal to the surface of the pulp canal at each stage of growth, the shape of the tubules reflects the orientation of the dentine crystallites. This means that the dentine tubules must be standing in a radial array over the top of each pulp canal, and hence the arrangement of the crystallites in that region is only partly radial around the point marked by the top of the pulp canal. As can be seen from Fig. 69C and from Gross (1956: pl. 10, fig. 3), the branching and the bending of the tubules allows their ends to be arrayed normal to the surface of the flask chambers, reflecting the radial arrangement of the crystallites with respect to the flask walls. The arrangement of the tubules at the different levels in the cosmine is illustrated diagrammatically in Fig. 75.

As has been indicated above, at a deeper level in the cosmine the concentric layering of the dentine around the pulp canals becomes obvious (Fig. 71A). This is because growth in the later stages of deposition was restricted to the narrow cylinders around the canals. Before these cylinders were formed, the spaces between the successive positions of the cylinders had been occupied by dentine deposited from much larger pulp canals, whose form can be inferred from the variously oriented branched ends of the dentine tubules. Because the earliest dentine was deposited around the flasks, and it had to be deposited from a pulp canal, the walls of each flask were contributed to by three or four different pulp canals (Fig. 75B,C). This inevitably results in zones of interference between neighbouring pulp canals. These zones are stippled in Fig. 75B,C. Thomson (1975) referred to this tissue formed in the interference zones between the cylinders as 'interstitial dentine', a name that he also applied to the dentine formed over the top of the pulp canals. We see no need for a separate term for this dentine, which is really only the result of the changing shape of the pulp canals during growth (Figs 72A,B; 75).

The dentine overlies a coarsely vesicular bony layer (the spongiosa of Gross, 1956, and Thomson, 1975) that usually extends across the whole width and length of the scale, although it is missing in the overlapped zones of some specimens. The vesicular layer consists of one to three irregular layers of vesicles. If the vesicles are of more than one size, the largest ones tend to occur at the base of the layer (Figs 68B,C; 70B,C); in addition

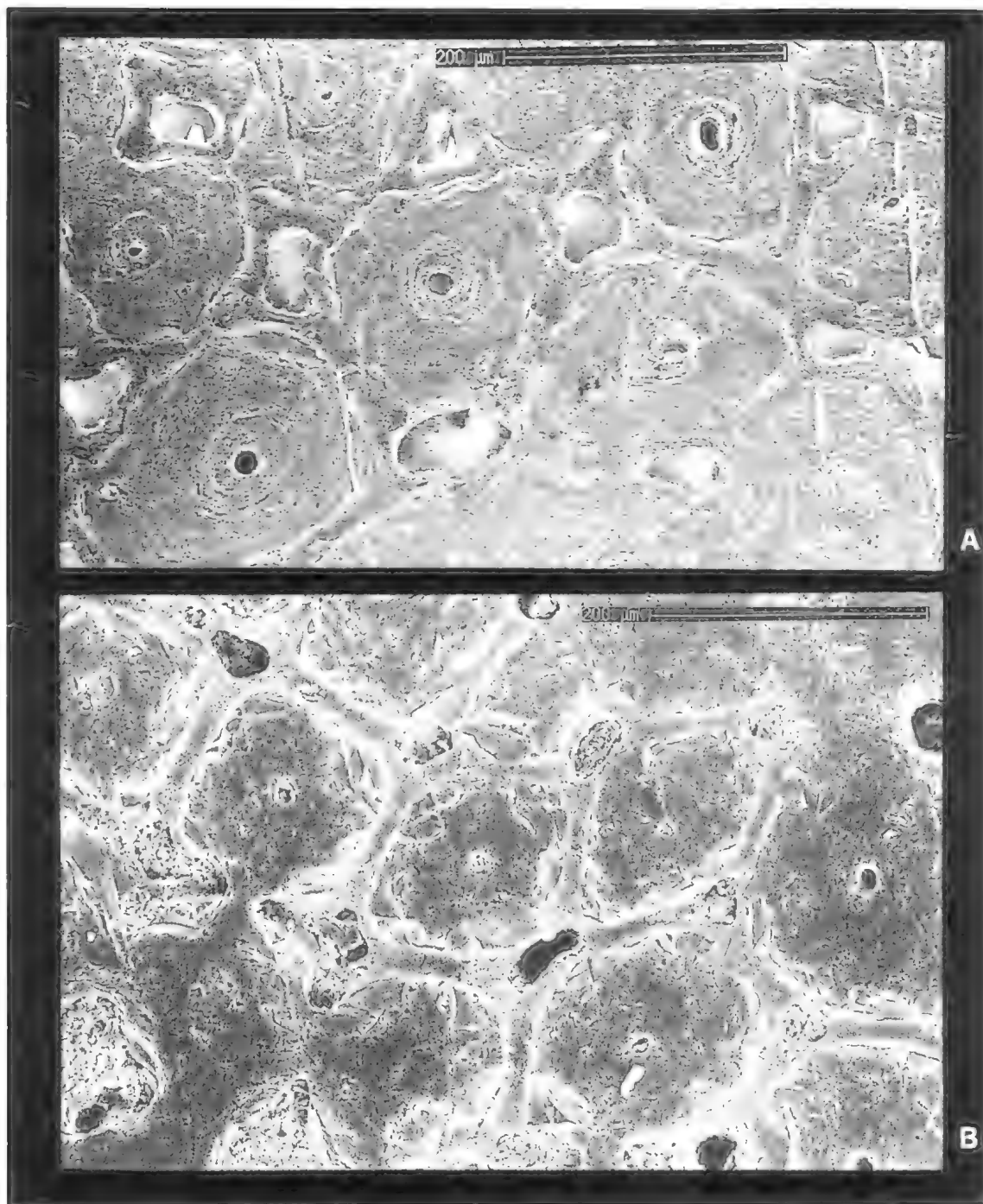


FIG. 71. *Cladrosymblema narrienense*. A,B, two SEMs of a polished horizontal section of a scale, QMF33052, cut near bases of flask chambers. In each, small holes are the pulp canals which are surrounded by concentric layers of dentine. In A, which is cut a little deeper into the scale than B, highly irregular bases of the flasks are well seen, in places also showing the mesh canals. In B, mesh canals are almost complete. The bottom left of the photo is slightly above the mesh canals and the top right is below them. Both sections are from polished surfaces etched for about 90 seconds in 1% HCl.

there is a tendency for the size to decrease marginally. Within the overlap area, the vesicles have no preferred size.

The basal layer is made of dense lamellar bone that is added both marginally and at the base of the scale. Sections through the overlapped part of the scale show that the lamellae fold around from the internal to the external surface (Figs 69A,B; 73A), indicating that they were laid down from the tissue of the enveloping scale pocket. At the scale margins, where the lamellae can be followed around from the basal to the external surface, only the outer layers are complete, the inner layers being truncated against the vesicular layer where it is present, as is shown in the above-mentioned figures. The vesicular layer in this marginal zone tends to lose its coherence, and towards the outer limit the vesicle size becomes small. This implies that the vesicular layer expanded marginally by resorbing the lamellar layer, which it then replaced, the vesicles gradually growing in size as growth removed them from the marginal area.

The lamellar layers were added as sheets to the inner surface of the scale. Their internal structure is distinctive as is well shown under crossed polars and in SEMs. Under crossed polars, alternate layers go into extinction almost as a unit, indicating that these layers are composed of crystals set normal to the surface. In plane polarised light, each layer is seen to be crossed by fine lines that may define the crystal boundaries, but the lines are marked by films of iron oxides, suggesting that they may be infillings of very fine pores. Scanning electron micrographs show no sign of such pores, but can be interpreted as supporting the vertical crystal hypothesis (Fig. 73C). The alternate lamellae show no such pattern under crossed polars, being partly extinguished in all positions. Presumably, therefore, the mineralising tissue has the capacity to change its mode of action in a regular way during growth. This must be in some way related to the orientation of the fibres in the collagen, the mineralisation of which has been referred to above. Gross (1956: figs 33A; 35A) illustrated this phenomenon in other osteolepiforms. He referred to the vertical crystal layers as 'quergetroffenes Fasserbündel', and the

alternate layers as 'längsgetroffenes Fasserbündel'.

The contact between the vesicular and lamellar layers over the width of the scale does not follow the boundary of a single lamellar layer. Instead, several basal lamellae are truncated obliquely against the vesicular layer (Fig. 69A,B). At several points the wall of a vesicle can be seen to have increased its thickness at the expense of the adjacent lamellar layer (Figs 68C; 70B). Some resorption of the latter must have taken place to allow the vesicle walls to grow.

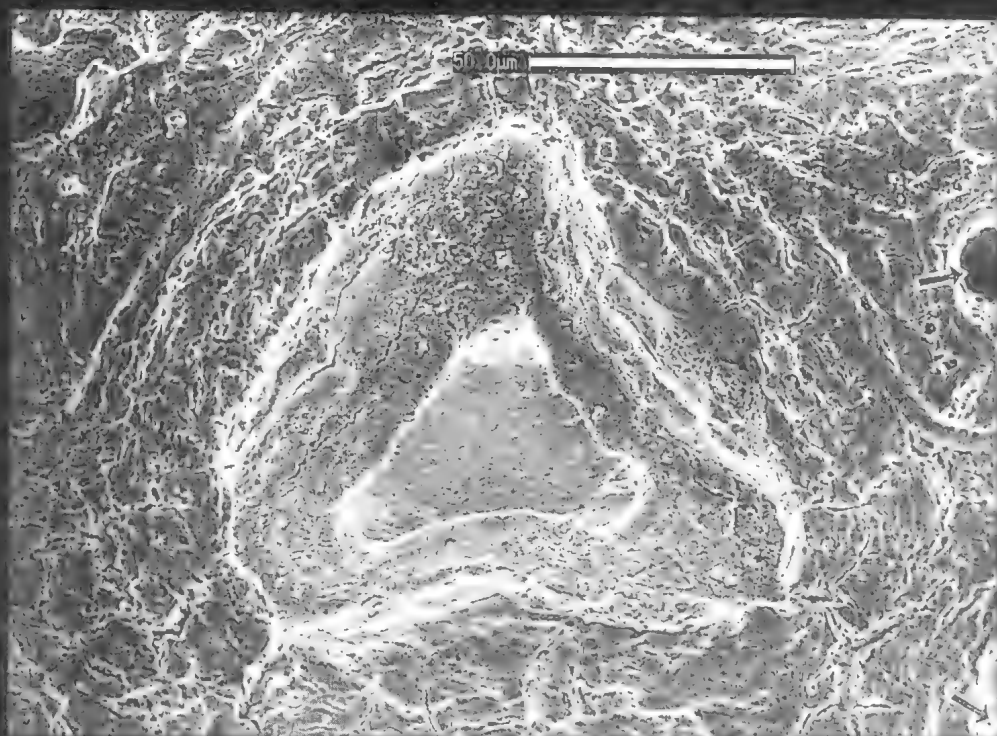
As indicated in the section on gross morphology of the scales, some of the layers fall free during acid preparation, and we have attributed this to the absence of mineralisation in some of the lamellae. Thin sections tend to confirm that interpretation. As shown in Fig. 70B, gaps are completely conformable with under- and overlying lamellae, which in turn show no corrosion. This pattern would be difficult to produce by selective resorption. On the same thin section, patches of resorption are present and are easily distinguishable. Hence, we prefer the non-mineralisation hypothesis.

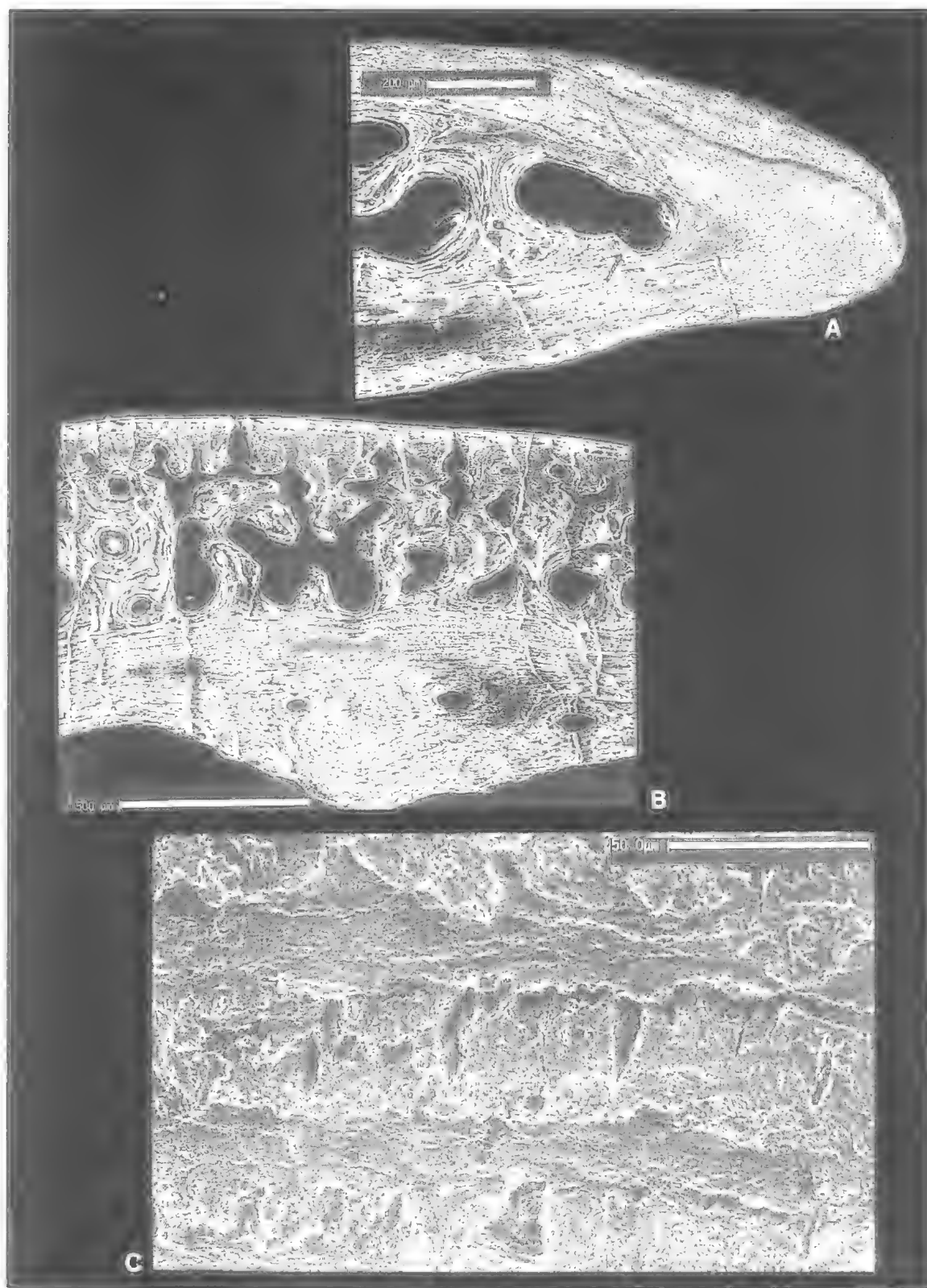
Sections of the ridge on the inner surface of some scales show that it was not formed by thickening of one or more lamellar layers. Instead, it is a highly discrete structure that is composed of thin layers showing complex folding and radial features of unknown origin (Figs 68B,C; 73B).

Scale Growth. Several of the above features provide clear indications of the mode of growth of these scales. The absence of Westoll lines in the cosmine, the presence of infolded edges of enamel around the cosmine margins, and the absence of older enamel rims incorporated in the cosmine, indicate that the enamel margins were completely resorbed during growth phases. On the other hand, thin sections show no sign of discontinuity within the cosmine itself. As we can find no evidence of the resorption of the cosmine layer from a whole scale at any one time, the only conclusion seems to be that the downfolded enamel margins were resorbed in advance of growth.

Resorption patterns on the scales vary tremendously. Examples are shown in Figs 66-67. A

FIG. 72. *Cladarosymblema narrienense*. A,B, SEMs of the dentine layer of the cosmine in a scale, QMF33051, prepared from a polished section cut down to just below the base of the flask chambers. A, the base of a flask chamber with adjacent pulp canals (arrows). B, pulp canal with adjacent flasks (arrows). The flask at the bottom left of the figure is the one shown in A. The concentric layering of the dentine around the pulp canal, and the so-called interstitial dentine of Thomson (1975) are apparent. In the interstitial dentine note the well-defined sub-circular pores, 0.5 - 2.5 microns in diameter, towards the bottom right of the figure where the dentine tubules have been cut across obliquely.





pattern of resorption has been clearly established. First the enamel layer was removed from a patch on the surface (Figs 66A; 67A,B,D). Presumably this could be accomplished only by the action of the overlying dermal layer. Then removal of the dentine layer began progressively from the inner edge of the area from which the enamel had been removed. This progression was marked by an increase in the size of the flask chambers (Figs 66A,B; 67A,D). Such increase in size could be produced by two different processes. The first involves the removal of layers of dentine from the surface by continued action of the dermis, thus exposing progressively deeper sections through the flasks; this seems to have been the case in Fig. 67D, which gives the impression that the dentine surface was progressively lowered until the mesh canals were exposed. Alternatively, it could result from resorption of the inner walls of the flasks by osteoclasts housed within the flasks; where this occurred the inner walls of the flasks show progressively more irregular shapes as they increase in size (Fig. 66D), and eventually a point was reached where all the dentine was removed along a sharply defined vertical edge, indicating that resorption was taking place from beneath the dentine. This alternative view is espoused by Borgen (1989, 1992). The shape of the resorbing front indicates that osteoclasts were located not only in the flasks, but also in the underlying bone spaces. Indeed Borgen reached a similar conclusion, but tentatively identified the deep source as the pulp canals. We see no evidence in our material of the involvement of the pulp canals. Thus it seems that resorbing cells were located in the epidermis, in the tissue lining the flask chambers, and in the bone spaces.

The specimen in Fig. 66A,C,D shows three phases of cosmine growth. The oldest phase is the most extensive, but the thinnest; it covers most of the cosmine surface and is labelled 1. The second oldest is in the central patch, labelled 2. Some of its edge is still entire but other parts show evidence of resorption (Figs 66A,C; 70A). The youngest, labelled 3, forms the almost complete annulus around the centre; it was growing both

centripetally and centrifugally, and its margins are entire everywhere. In Fig. 66B the annulus seems to have formed from more than one centre. Details of this figure are given in the caption to the figure itself. Several other scales show quite different patterns (see Fig. 67A), and some of them have only tiny areas of resorption or none at all. Space forbids the illustration of the full range of variation in cosmine growth that we have observed.

As mentioned in the description of the gross morphology, there is a gutter between the cosmine and the overlapped part covered by lamellar bone. Vesicular bone is normally, but not invariably, exposed in this gutter. For the area of cosmine to expand in the direction of the overlapped part, resorption of the free edge of the lamellar layer against the gutter would have to take place in advance of the growing front, thus exposing the vesicles. That some of this resorption went deeper than the surface is demonstrated by the occurrence in the gutter of vesicles with their tops removed (Fig. 69B). In other scales, the continuity of the lamellar layer of the overlapped surface to the edge of the cosmine, shows that resorption was lagging in at least some individuals. This variation could indicate different stages of growth rather than individual differences.

TEETH AND TUSKS

In addition to the teeth in the jaws, the matrix has yielded several isolated teeth and tusks. We have been able to section and study some of these in isolation. The infolding of the dentine and enamel is simple and, as in other osteolepiforms, it is polyplocodont (Schultze, 1969; Warren & Davey, 1992: 118). The folding reaches less than half way up the tusk from the base. The surface layer of the tusks is covered with very fine anastomosing longitudinal striations (Fig. 76B,C). As is normal for osteolepiforms, these are best developed towards the base of the tooth on the outfolds of the enamel and dentine, but can still be traced almost to the tip. At the base they are spaced c.60 per mm transversely, which is about four or five

FIG. 73. *Cladarosymblema narrienense*. A, SEM of the overlapped part of a scale, QMF33053. Note continuity of the lamellar layers around the margin, breakdown of the lamellae in advance of the growth of the vesicular layer, and how newly-formed rings around the most lateral vesicle cut the lamellae of the lamellar layer (arrow). B, deeply etched vertical section through the ridge on the inner surface of the same scale. Note laminae in the enamel, irregular orientation of the cross canals, continuity of the lamellae of the inner layer between the vesicular layer and the ridge, and internal irregularity of lamellae in core of the ridge. C, SEM of part of the lamellar layer of a scale, QMF33053, to show the different orientation of the crystallites in alternate layers. The surface was polished and etched in 1% HCl for about 90 seconds.

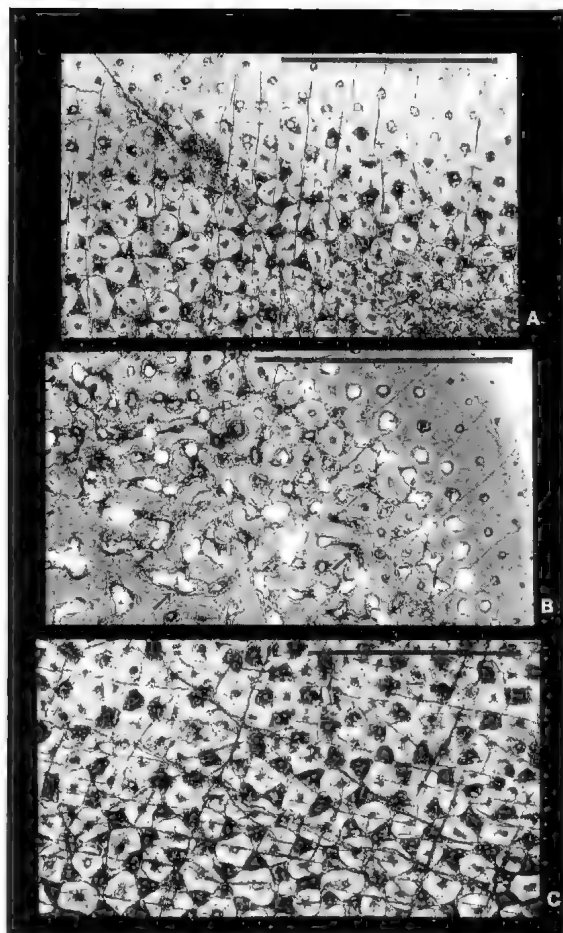


FIG. 74. *Cladarosymblema narrienense*. Thin sections of scales showing shape variation in elements of the cosmine layer and immediately underlying bone. A, B, sections slightly oblique to scale surface; outer edge of scales to the upper right. Narrow openings into flask chambers become progressively greater in diameter away from the edge; mesh canals then become obvious. A, many flask bases are filled with a ferruginous compound. Annuli of dentine around pulp canals are obvious. Dark spots in the annuli of A indicate that the level of true bone has been reached; cf. Fig. 70C. B, more obliquely cut, bases of dentine annuli open out into crude and irregular cross-canals (arrows). C, QMF31901, section is cut mostly through level of the mesh canals, which are filled with an iron compound. Note also fine radial dentine tubules in dentine columns. Scale: 1mm.

times the number found in *M. hibberti* (personal observation).

A tusk broken from the holotype, and two other isolated tusks, have been transversely serially sectioned. Sections from the former series are figured as Figs 77A,B and 78A,B. At the base of

the tusk, the pulp cavity is very wide and is surrounded by a thin layer of folded dentine. In places the folds themselves are slightly folded (Fig. 77B). Progressively higher on the tusk, the dentine thickens rapidly and the folds are more clearly defined. Towards the base of the tooth, the gaps between the folds are crossed by tissue isolating as many as four spaces (Fig. 77B). This crossing tissue is honey-coloured like the dentine, but it contains no dentine tubules. Presumably it is bone of attachment, a view that is supported by the fact that further up in the tusk this 'crossing tissue' disappears and the folds are open to the external surface.

The surface of the tusk is covered by enamel in most specimens. Where it is clear (Fig. 78C,E), the enamel is usually thin in comparison with that on the tusks of *Megalichthys* sp. figured by Smith (1989). In others it has broken down diagenetically, as shown in Figs 77A; 78A,B). The enamel shows little lamination in transverse and longitudinal section (Figs 78C; 79A), and we have not been able to produce details of crystal bundles similar to those produced by Smith (1989: figs 13-14) for *Megalichthys*. This could be the result of preservation or of faulty technique, rather than absence of the tissue in question.

Immediately beneath the enamel is a thin but distinct layer of so-called globular dentine within which the tips of the dentine tubules ramify (Fig. 78C,E). This is very similar to the layer in *Rhizodus* and *Megalichthys* figured by Smith (1989: figs 8A,B; 14C). Its presence throughout the length of the tooth cannot be established with certainty, but we consider that such a distribution is most probable.

Towards the distal part of the tusk, near the limits of and beyond the region of folding, transverse sections show the dentine tubules closely packed and dividing repeatedly towards the outer surface. In thin sections they seem to maintain their diameter throughout (Figs 77; 78), but as the SEMs reproduced in Figs 79C & 80 show, this is not always so. In Fig. 80C, for example, the tubules decrease in diameter considerably lateral to the division points and remain that way to the tooth margin.

The dentine tubules in the proximal sections of the tusk are straight or slightly curved to accommodate to the differences in shape between the inner and outer surfaces (Figs 77A,B; 78A,B). In vertical sections the tubules are straight to slightly curved, and in the basal part of the tooth are oriented at approximately 70° to the external surface; as is required by simple geometry, the

tubules are progressively more acute to the external surface towards the tip of the tooth. In optical thin sections the tubules seem to be similar to those of *?Megalichthys* figured by Schultze (1969: pl. III) and those of *Megalichthys* sp. figured by Smith (1989: figs 12A-C) in their close spacing, their orientation and their diameter. On the other hand, they are unlike those figured by Gross (1956: fig. 119, pl. 14, fig. 4) for *Latvius grewingki* in their spacing, in the obvious combs of fine tubules between the main ones, and in tubule diameter. However, SEMs show a variety of tubule morphology in *C. narrienense*. Although some of this variety could be the result of our failing to recognise different taxa in the collection, it is considered more likely to be the result of different phases of growth under different environmental conditions in the one taxon.

One of the noteworthy features of the teeth is the extent to which they show variation in growth. Three distinct types of growth laminae are known:

(1) The first involves major breaks marked by layers of amorphous tissue that survives etching in HCl. In some specimens such breaks mark total reorganisation of the tubules as shown in Fig. 79B,C; in others the branching pattern and diameter of the tubules changes as in Fig. 80E; and in still others the tubules are comparable on both sides of the break but they are not aligned on opposite sides. In thin sections it is not possible to discriminate structure within the tissue defining the growth halts, and in SEMs the breaks stand up as structureless walls as is shown in the above-mentioned figures. The tubules cannot be traced across these boundaries. During preparation it is not uncommon for the tooth to break up along these surfaces (Fig. 76D). The specimen of *?Megalichthys* figured by Schultze (1969: figs 1a, 1b, 3a) shows breaks of this kind.

(2) The second type is seen in optical thin-sections as dark coloured bands through which at least the major canals can be observed to pass (Figs 77A; 78A). These breaks are not so strongly marked as those of type 1. SEMs of these boundaries indicate that at least some of them are distinguished by changes in the branching pattern of the pulp canals (Fig. 80C,D). This type of surface apparently indicates the initiation of a new growth phase.

(3) The third is minor in comparison with the other two, and is recognised by thin sheets of some unspecified tissue that survives etching in HCl; these are closely spaced, and usually mark surfaces across which bifurcation or trifurcation

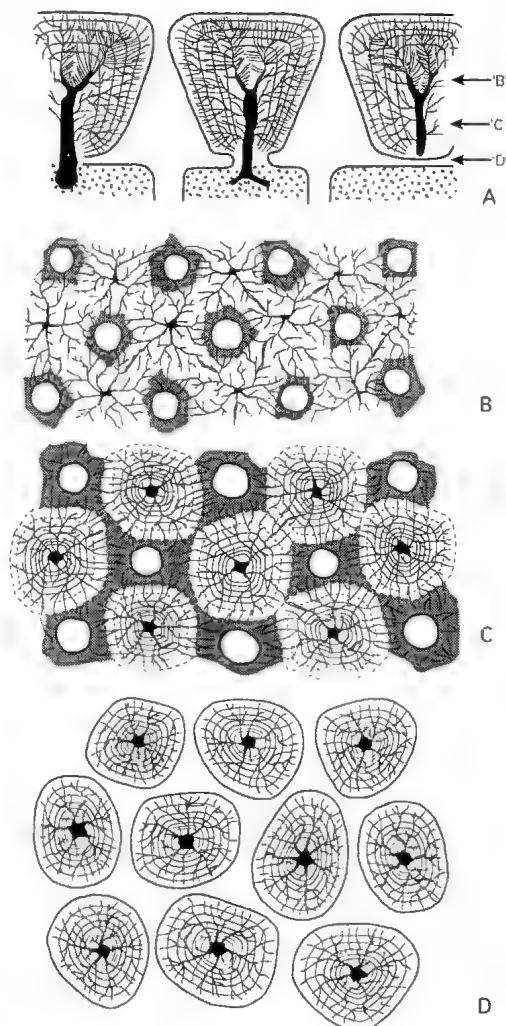


FIG. 75. *Ciuruarosymblema narrienense*. Diagrammatic reconstruction of the cosmine of a scale. A, vertical section through two flasks and three pulp canals, showing the postulated growth lines in the dentine, the orientation of the tubules, and the osteocyte spaces at the base. Positions of sections B-D indicated. B, horizontal section cut at the top of the pulp canals. The stippled areas are Thomson's (1975) interstitial dentine; compare Fig. 69C. C, section cut half way down the pulp canal; compare Fig. 72B. D, section through the mesh canals; compare Fig. 71A-B.

of canals occurs (Fig. 80F). There is no interruption of canals at these boundaries, which are spaced at intervals of c.5 microns.

The different types of growth laminae are not mutually exclusive in teeth. For example, those

of the third type occur on the same tooth as the major breaks of type 1 above.

Our interpretation of the significance of these variations is inadequate, and needs much more work. It is in part hampered by the fact that our material is not from known positions in a jaw, and we are unable even to say if any one specimen is a small tusk or a large tooth. As a consequence, it is not possible to indicate if all the teeth and tusks in a single animal have a similar range of structures. At first sight, it is reasonable to conclude that there were major interruptions to the life history of many animals during which growth ceased, and following which reorganisation of the tubules took place. These could have been events such as droughts. Other animals need not have suffered such major changes, but nevertheless did experience lesser changes that produced the structures of type 2. Seasonal changes suggest themselves as an explanation. The minor breaks are possibly daily increments.

FUNCTIONAL INTERPRETATIONS

SWIMMING

Little attempt has been made to interpret the swimming mode of rhipidistian fishes since the work of Thomson (1969), although Ahlberg (1992) has commented on the porolepiforms, and Belles-Isles (1992) has examined both osteolepiforms and porolepiforms in this respect. Both these treatments dealt primarily with the caudal region of the animal, which our material lacks. Hence we have been forced to attack the problem independently, using such features as the scale structure and pattern, the body form, and the shape and structure of the pectoral fins.

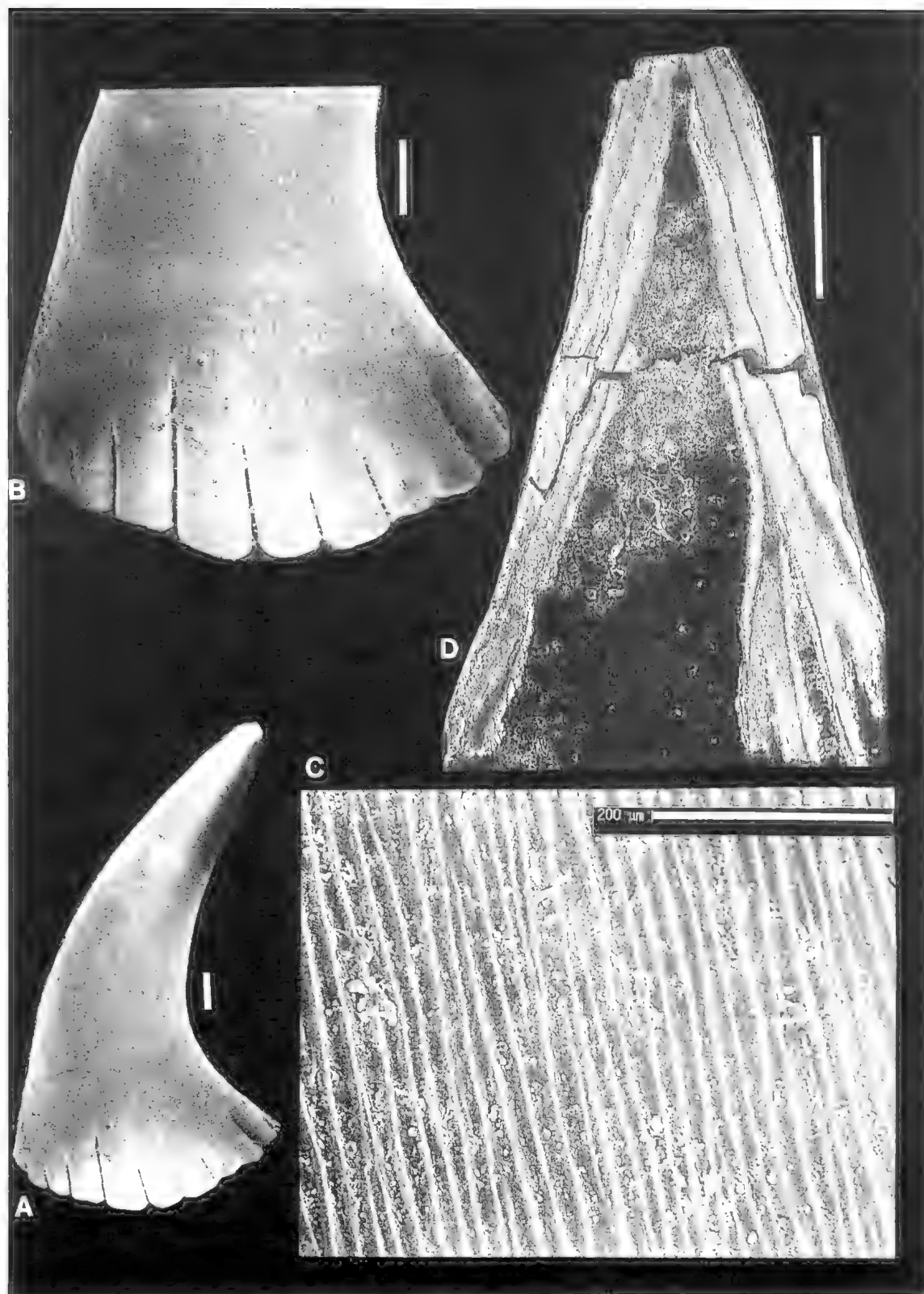
Scales and Body Form. The exposed area of each flank scale is large relative to the total scale size. The scales show no sign of a peg and socket articulation. The overlapped areas are convex rather than flat, and thus provide a neat surface over which the adjacent scales could slide during flexure. The presence of a gutter between the overlapped and exposed parts of the scales provided a groove into which the cosmine-covered edges of the adjacent scales could tuck when the body on that side was on the concave side of a flexure. These features suggest that the entire post-cranial body was flexible. The short ring

centra, which demonstrate a large number of bending units, also suggest body flexibility.

The holotype is the only articulated specimen we have, and it is depressed. However, the mode of flattening, the reconstruction of the cross-section of the head at its posterior end, and the number of body scale rows, indicate that *Cladarosymblema* was not a deep-bodied fish. In addition we have an uncrushed pectoral girdle with a flat-sided dorsal part and a relatively sharply inflected ventral part of the cleithrum, together with a flat clavicle. From this information we conclude that the body was somewhat flattened ventrally in the immediate post-cranial position, a view that is supported by the shape of the large gulars. The preserved part of the holotype, which is 28cm long, and 19cm long behind the otico-occipital unit, shows no sign of the anterior dorsal fin, which therefore must have been posteriorly situated on the animal. If allowance is made for the two dorsal fins and the caudal fin, we estimate that the total length of the fish would have been c.40cm. Estimates of the vertical and horizontal axes of the body behind the pectoral girdle are 6.5 and 7.0cm respectively. Hence the fish must have been long and slender. Having taken account of the previous argument that the body was generally ovate in section, although somewhat flattened ventrally towards the front, and that the body was flexible throughout, we consider that the total design would be consistent with subcarangiform movement. This, together with the posterior position of the median fins, suggests that the propulsion was predominantly caudal. Such an arrangement is consistent with a life style that requires slow movement over long periods and short bursts of high acceleration. However, no conclusion can be reached without a consideration of the pectoral fins.

Function of the Pectoral Fins. The pectoral fins are different from those of any other osteolepiforms with which we are familiar, except perhaps for *Megalichthys hibberti* itself. The fins of that species have not been well photographed. Andrews & Westoll (1970b: pl. 4, fig. A) have figured a relatively complete right fin that has many features shown by *Cladarosymblema*, although the boundary between the basal scales and the ray scales is not as sharp.

FIG. 76. *Cladarosymblema narrienense*. All SEMs. A, isolated tusk, QMF31906. B, enlargement of base of same. C, enlargement of the surface of QMF31907 just above the zone of folding. D, deeply etched vertical section of a small tusk, QMF31905. Note the section through the deep folds at the bottom right, and the strong growth breaks (compare Fig. 77B). Scales: A,B,D, 1mm.



The basal lobes of *Cladarosymblema* are unusually broad, and their extremities are broadly rounded rather than tapered to a point. The number of dermal fin rays is very large, and they are all contiguous, leaving no space for membranes between the rays. Unlike other osteolepiforms, long rays extend around the trailing edge of the fin almost as far as they extend around the anterior edge. This produces a large, flat, paddle-shaped structure. Such a fin shape would not be for propping the animal on the bottom, but was either for swimming in a steady fashion, or for orienting the animal during rapid movement. The problem of distinguishing between these options can be approached either by comparison with other lobe-finned fishes such as *Neoceratodus* or *Latimeria*, or by direct hydrodynamic considerations.

A second important feature bearing on this issue is the position of the fins, which are placed in a low position on the body at an angle formed by the sharply rounded flexure of the cleithrum. This means that the fins would apply a force low on the body, below the centre of gravity. Modern actinopterygians that use the pectoral fins for locomotion rather than orientation, are usually deep-bodied, with fins attached high on the side of the animal (Webb, 1982). This applies equally well to those that use their fins for 'rowing' and to those that use them for 'underwater flying'. Hence the body shape and pectoral fin position suggest that these fins in *Cladarosymblema* were not primarily locomotory.

A third point is that, being situated on a sharply rounded flexure in the body profile and having such a thick proximal lobe, it would be difficult to fold the fins back smoothly against the body. This suggests that they could not easily be rotated out of the water flow at continuously high speeds. Although this argues against long-continued fast swimming, it does not eliminate the possibility of short bursts of high acceleration. In such circumstances the large fins would be useful for directional change.

The basal lobes are covered with scales that decrease in size distally, show no evidence of significant overlap between scales, and have no peg and socket articulation. We have found no evidence that the lobes had an ossified axial skeleton; presumably the skeleton was cartilaginous, and therefore relatively flexible. Although the basal lobes were long and thick, they presumably retained some flexibility. So far as can be determined from the inadequately preserved specimen, the attachment of the fin to the body was

broad and thick, thus limiting the capacity of the fin to rotate about its articulation with the shoulder girdle. In all these respects it seems to be similar to *Latimeria*. However, that is where the similarities end. The fins in *Latimeria* are situated higher on the side of the fish than in *Cladarosymblema*, and the fin pattern is different in the two genera. In *Cladarosymblema* the fin is paddle-shaped and the rays are covered with a double layer of closely spaced cosmine-covered scales that are set in juxtaposition, whereas in *Latimeria* the fin is drawn out to a point, the rays are less numerous, more widely spaced, separated by membranes, and made of a vast number of very short lepidotrichs. Consequently the distal parts of the fins would have been more flexible in *Latimeria* than in *Cladarosymblema*. Fricke et al. (1987) have reported that *Latimeria* does not use its fins for walking on the bottom, but is able to use its paired and unpaired fins for generating thrust. The paired fins are also used to stabilise and correct drift motion in up- and down-welling currents. It is highly unlikely that such drift was a factor in the life of *Cladarosymblema* in semi-permanent shallow bodies of fresh water. *Latimeria* uses its paired fins in generating thrust by adopting an 'underwater flying' fin motion. Fins that are functionally adapted for such motion tend to have a high aspect ratio and are situated on the flanks of the animal, features not shared by the fins of *Cladarosymblema*. Consequently we are unlikely to be able to gain much information from an analysis of *Latimeria*, and again we are forced to make a judgment on the basis of hydrodynamic considerations.

Finally, it is as well to use the geological data to assist with interpretation of the animal's function. The inferred habitat of semi-permanent pools of fresh water suggests that persistent (steady) swimming was unlikely unless swimming against frequent floods was selected for; we note, however, that the sediment and the distribution of the strata indicate that the water was normally quiet and that flood events were infrequent. If they were frequent, it would be difficult to account for the concentration of the carbonate and the algal overgrowths that must have required long-continued stable conditions. In such an environment, the feeding type is more likely to be at a premium in controlling the design of fins. This fish was a carnivore, with tusks in the anterior part of its mouth for penetrating and holding active prey. The associated fauna shows that there was an abundance of actinopterygians of various sizes available as prey. This suggests an emphasis

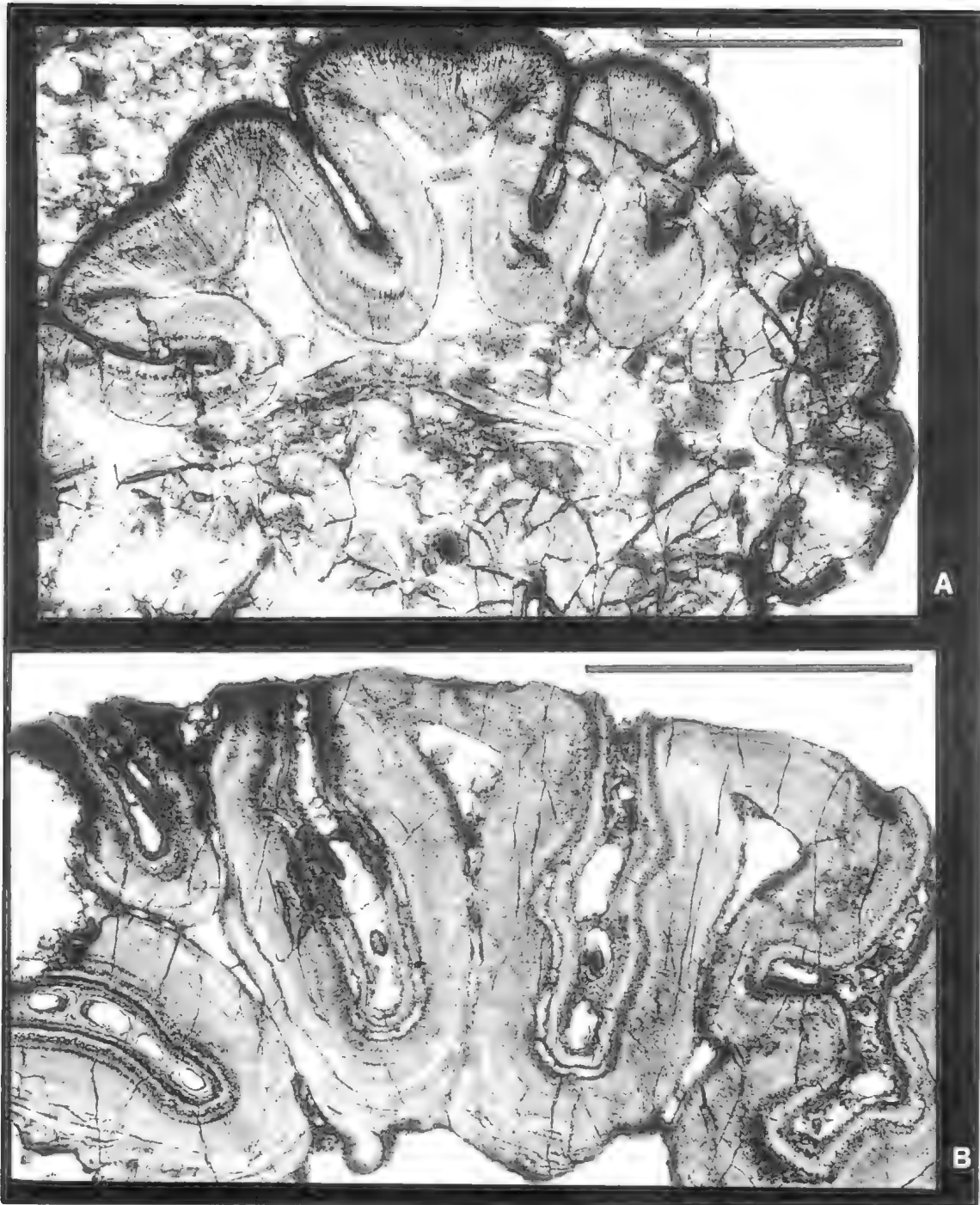
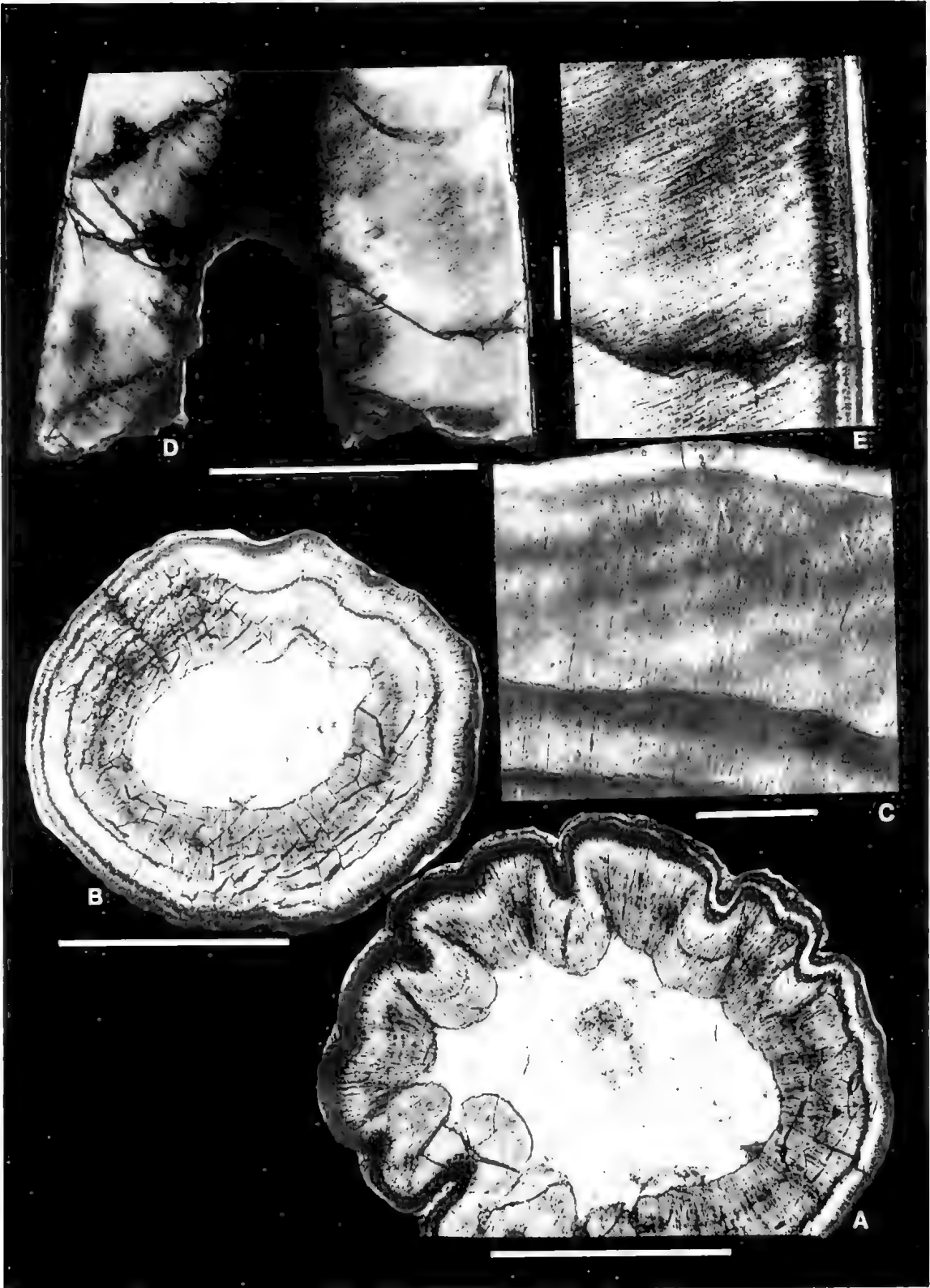


FIG. 77. *Cladarosymblema narrienense*. A,B, transverse sections of tusks, taken near the base. A is more distal than B. A was broken from the holotype, but the thin sections are numbered QMF31907. B, separate tusk, QMF33046; note the cross-bars of bone of attachment in some of the infolds (arrows), and the more complex folding on the right. B also shows two growth breaks towards the outer surface of the tusk. The dark layer around the outer surface in A, where the thin layer of enamel should be, is apparently the result of diagenetic destruction of the surface layers. Scale: 1mm.



on fast starts and abrupt turns. A similar view was espoused by Andrews & Westoll (1970b: 481) who commented that 'Some of the osteolepids seem to have been lurking predators . . .', and that they lived in environments where they could avoid strong currents ' . . . where sustained strong swimming would have been necessary'.

Thus, by a process of elimination, we are left with the view that *Cladarosymblema* was a fish that was propelled by subcarangiform movements, was generally a slow mover, but was capable of considerable acceleration in short bursts, during which time it had an excellent capacity to reorient itself in the water using its pectoral fins. This hypothesis is to some extent supported by the caudal fins of the new genus described from Norway by Ulf Borgen, and it could be tested by the discovery of the more posterior median fins of *Cladarosymblema*.

FEEDING

Discussion of biting and feeding in rhipidistians had been dominated by what authors concerned think of cranial kinesis. Thomson (1967) has given an extensive discussion of the pro-kinetic position, and Jarvik (1942, 1980) has advocated the non-kinetic position. We see no point in adumbrating these well-worn arguments, particularly as our material provides no additional information on the nature of possible movements of the intracranial joint. We will focus on the significance of features that have been relatively ignored by previous workers.

Musculature of the Mandible. The large adductor fossa in the mandible is indicative of large adductores mandibulae. This view, if it needs support, is corroborated by the large space under the otico-occipital roof to provide space for the contraction of adductor muscles. There is no doubt that the animal had a massive bite.

Judging from the size of its attachment area, the coracomandibularis muscle (see above) must have been powerful. But did it serve to depress the mandible? Lauder (1980b) has shown that in *Latimeria* the line of action of this muscle was above the jaw articulation when the jaw was closed, and therefore it cannot have been used to initiate jaw opening as it does in many

actinopterygians. He also noted that as the jaw opened, although the line of action dropped below the articulation and therefore is seemingly in a position to contribute to the later phases of depression of the mandible, this does not occur. With the downturn of the posterior end of the mandible in *Cladarosymblema*, it is difficult to be certain if the line of action would have passed above or below the articulation, but we consider it probable that the situation was similar to that in *Latimeria*. Lauder showed that electromyograms indicate that the prime function of the coracomandibularis is compression of the buccal cavity rather than opening the mouth. That leaves the sternohyoideus muscle as the main depressor mandibulae, but we are unable to comment on that muscle in the absence of the ceratohyal in our material.

The retroarticular process in *Cladarosymblema* is large; in *Latimeria* such a process serves for the attachment of the anterior and posterior mandibulohyoid ligaments. The former is attached to the hyomandibular and the latter to the symplectic. The surface of the process in *Cladarosymblema* displays two areas that could well have been for the attachment of ligaments. As Lauder (1985) has shown, in primitive teleostomes the mandibulohyoid ligaments mediate mandibular depression, and so this seems to be an appropriate function for these structures in *Cladarosymblema*. The large, anteriorly tapering muscle scar along the Meckelian bone ventral to the edge of the posterior face of the prearticular, has been interpreted as an attachment for strong posterior intermandibularis muscles. These would have extended as a sheet across the top of the posterior end of the gulars, and would have served two main functions; the constriction of the floor of the branchial cavity thus forcing water out across the gills, and helping to control the two mandibular rami during a biting strike at a large item of prey (see below). Smaller areas of attachment for the anterior intermandibularis muscles have been identified near the front of the mandible, and these would also have served to control the movement of the symphyseal part of the mandibular rami during a strike.

FIG. 78. *Cladarosymblema narrienense*. A,B, transverse sections through the more distal parts of holotype tusk (QMF31907) illustrated in Fig. 77. B is more distal than A. C, transverse section of part of another tusk, QMF33046A, showing unusually thick enamel and branching tubules in the mantle dentine immediately beneath it. D, vertical section through base of a tusk (QMF33047) cut between folds. E, enlargement of right side of same, photographed under crossed polars, showing enamel layer and multi-layered nature of immediately underlying dentine. Scales: A,B,D, 1mm; C,E, 0.1mm.

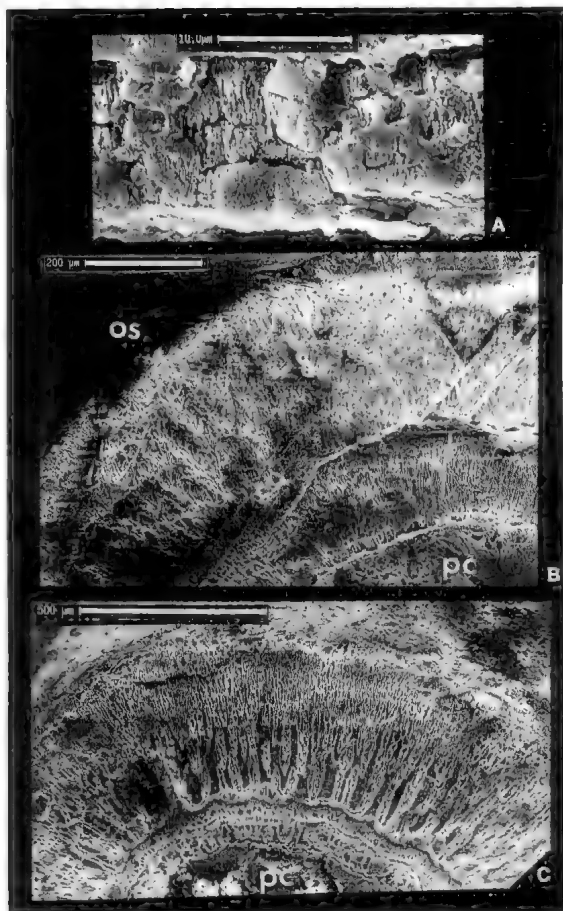


FIG. 79. *Cladrosymblema narrienense*. Specimens all lightly acid-etched; SEMs. A, enamel layer of a tusk, inner surface to bottom. Note the poor lamination and the lack of obvious bundling of crystallites. B, transverse section of tusk, QMF33049, distal to the zone of folding. Note the more or less regular tubules to the bottom right separated from the peculiarly arranged pattern of the outer layer by thick structureless wall of tissue. C, similar section through another tusk, QMF33048, showing disrupted growth around the pulp cavity, and ramifying tubules in the thick outer dentine layer. (pc = pulp cavity; os = outer surface.)

Movement of Mandibular Rami during Biting.

As indicated in the above description, the median symphysis was probably completed by a cartilage pad which would have allowed a degree of flexibility between the jaw rami. This conclusion is in agreement with two other aspects of the anatomy of the mandible. The first is the presence of the small, rhombic, loosely attached plate between the infradentaries, alluded to above. Secondly, the glenoid fossa is divided into two distinct surfaces of articulation, and if the median

symphysis is held vertically the inner half of the fossa is at a lower level than the outer. As a result, the load during biting could have been carried in one fossa or the other depending on stress distribution. The two glenoid surfaces are much more similar in size than those of Devonian dipnoans, in which the lateral surface is much the smaller of the pair. A paired arrangement of the articulatory surfaces is desirable under two quite different sets of circumstances. If, as in Devonian dipnoans, the mandibular symphysis was rigid and a large prey item was held on one side of the mouth, exertion of pressure would tend to dislocate the jaw articulation on the opposite side. Hence, a second glenoid articulatory surface would be desirable so that it would be able to carry the stress when the adductor muscles on both sides contracted. If a flexible symphysis were present, an entirely different mechanism would have operated. A large food item caught on one side of the mouth would cause the ramus on that side to rotate outwards and thus the articulation would jump from the outer to the inner glenoid fossa, the articulation on the opposite side of the animal remaining stable. Such a view is supported by the fact that the teeth on the mandible are turned slightly inwards so that they would be more effective when the ramus rotated outwards. The dipnoan design would be an advantage for an animal grinding its food on tooth plates because pressure could be exerted effectively on both sides of the mouth. The osteolepiform design would be an advantage for an animal holding and killing struggling prey by puncturing. It is probably significant that we have recovered from the fauna no invertebrates that could have provided a relatively passive food source, but there are large numbers of actinopterygians and acanthodians of many sizes that would have provided active, struggling prey.

A second factor related to both feeding and respiration has to be taken into account in any discussion of jaw movement. As Lauder has pointed out on many occasions (see especially Lauder, 1985), primitive aquatic vertebrates suck in their prey by rapidly expanding the buccal cavity. This is accomplished by three separate means - dropping the mandible, dropping the gular plates, and laterally expanding the quadrate/mandible articulation. This latter movement is possible only if the quadrate is mobile and if the mandibular symphysis is flexible. Hence, symphyseal flexibility is an important factor in both feeding and respiration. Lateral expansion of the jaw articulation is also a factor in explain-

ing the double glenoid surface. As pointed out above, the inner fossa is slightly anterior to, as well as lower than, the lateral one. Assuming that the articulatory process on the quadrate was also double, lateral movement of the whole would be facilitated if the articulation could jump from one surface to the other depending on the degree of lateral expansion. Obviously, feeding and respiration are intimately linked in fishes, and hence if the above hypothesis is of any significance, the positions of the articulations for biting and for respiration would have to be consistent. This means that because suction has to be at a peak at the time of a strike at prey, the articulation would be at maximum spread, and the inner glenoid would be engaged. This is the position of the articulation required when maximum pressure is exerted on prey. Such internal consistency is supportive of the above hypothesis.

SENSING THE ENVIRONMENT

Tubules in Snout. Tubules occur in the rostrum and in the symphyseal region of the mandible. They are not nearly so numerous nor apparently so inter-connected as those in the Dipnoi, nor do they have the same longitudinal arrangement. Foramina in the antorbital wall connect with these tubules in the same way as do the profundus and ophthalmicus superficialis nerves in extant and fossil dipnoans. These nerves are sensory, and are generally considered to have served electroreception systems. To have this function they would have to open to the external surface. In Devonian dipnoans these openings are numerous, but they are smaller than those for the lateral line canals. In our material, it is not clear that the tubules open to the exterior via a set of small openings, although there may be connections via the lateral line pores.

In the mandible of *Cladarosymblema* the tubules are restricted to the immediate inner surfaces of the dermal bones, and although they divide and penetrate these surfaces, they never make the diverse patterns seen in the Devonian dipnoans. Also they do not seem to connect with external openings in the dermal bone to anything like the same extent as do the tubules in the mandibles of Devonian Dipnoi. As indicated in the descriptive section, it is impossible to reach a definite conclusion on their function.

Special Cutaneous Sensory Pit Groups. These groups, consisting of between five and fifty pits, occur on the snout mesial to the narial opening, on the posterior nasal, the parietal, the supratemporal, the squamosal, the postorbital, the an-

terodorsal corner of the opercular and suboperculars 1 and 2, and near the vertical pitline on the mandible. Bjerring (1972: fig. 6A) made serial sections of part of a roof of *M. laticeps* that show that the small group on the supratemporal (his intertemporal) is served by fine canals connected directly to the lateral line canal in that bone. We have not sectioned a specimen, but X-radiographs show an abundance of relatively coarse branches from the main canal in the supratemporal. Although some of these branches are present beneath the pit groups, others extend well beyond the area covered by pit groups. The same kinds of comments can be made about the groups of pits in the ethmoidal unit. Hence, we can produce no evidence that the multiple branches from the main canals are involved with the supply of nerve fibres to the pit groups. It is unlikely that the X-radiographs would pick up structures as fine as those Bjerring figured.

Another way of approaching the problem of the necessary interconnection of the lateral line canals and the pore groups, is to examine the proximity of groups to lateral line structures. Jarvik (1948: 137) commented: 'No doubt the fine canals leading to the pores transmitted fine nerve twigs, and the position of the pores close to the sensory canals and pit-lines indicates that these nerve twigs are of lateralis branches'. Whereas it is true that the groups on the roofing bones and the squamosal lie close to either canals or pit lines, those on the opercular and subopercular do not. It may be significant, however, that the group on the opercular is in the anterodorsal corner where it would lie close to the lateral line in the preopercular; but even if this is accepted as significant, no such proximity can be argued for the pore groups on the suboperculars. We conclude that no necessary connection between the lateral line system and the pore groups has been established.

The function of these pit groups is unknown, but Bjerring (1972: 85) has speculated that they may have been thermal receptors. Why an organism living in the environment postulated for *Cladarosymblema* would need thermal receptors is difficult to understand. In any case we know of no modern analogue for such organs having such a distribution. It is unlikely that these pits would be mechanoreceptors, because on the ethmoidal unit and the intertemporals they are surrounded by normal neuromast pores, and hence subsidiary receptors of the same kind would seem to be superfluous. On the other hand, modern paddlefishes, which live in a riverine environ-



ment, do have clusters of ampullae distributed on the elongate rostrum, the cheek and the gill cover (Grande & Bemis, 1991: figs 1A-D). These are known to house electrosensory organs similar to the ampullae of Lorenzini (Jorgensen et al., 1972). The innervation of these structures remains unknown, but in other fishes the ampullae of Lorenzini are innervated from electrosensory fibres associated with the lateralis system. The pit groups in paddle fishes are far more extensive than those of *C. narrienense* and the analogy may be inappropriate; but two points give confidence that it has some merit: in *C. narrienense* some of the pit groups are associated with the lateral lines, and in paddle fishes, as in *C. narrienense*, clusters of pores occur on the gill covers, which carry no lateral line.

Should this interpretation be accepted, one residual point remains. That is, the cosmine between the individual pits retains flask chambers, which elsewhere in this paper are interpreted as having an electrosensory function also. The close proximity of the two types of receptor requires explanation.

Flask Chambers in the Cosmine. These structures have been interpreted as housing electrosensory organs (Thomson, 1975), osteoclasts (Borgen, 1988, 1992), or dermal papillae supplied by cutaneous blood vessels (Bemis & Northcutt, 1992). Another possibility is that they were the sites of mucus-secreting cells. In the descriptive section above we have concluded that osteoclasts functioned from the flasks, and that conclusion implies a blood supply. However, it does not imply that their only functions were resorptive. That they had additional functions is indicated by two other observations. First is the fact that pulp canals are spaced evenly between the flasks; these must have been supplied with blood to provide the nutrients for the deposition of the dentine, although not for the dermis on the external surface of the cosmine, because no dentine tubules penetrate the enamel layer. Hence the nutrients for the dermis outside the scale pockets

must have come from the flasks, the only structures that connected with the surface layers which, as shown above, must have had a blood supply. The blood would have been carried via the irregular deep cross-canals that made connections between the bases of the pulp canals and the flasks. The second important observation is the regularity of the mesh-canals between the adjacent flasks. Because we have already determined that a blood supply was available to the flasks via the cross-canals, the mesh-canals would be superfluous as blood conduits. In addition their regularity is not characteristic of a blood distribution system. Nor is it comparable with any mucus gland system of which we are aware. On the other hand, their array is reminiscent of the design of elementary sensory receptors such as are found in the compound eyes of arthropods. We can only conclude at this stage that the flasks served at least three functions: a nutrient supply to the dermis, sites for osteoclasts involved with the periodic resorption of the cosmine, and sites to house sensory receptor cells. Such receptors would not have been mechanosensory because the lateral line system was well developed, nor chemosensory because such a distribution is not known in any living organism. On the other hand, electrosensory receptors are widely distributed on the body of many aquatic vertebrates (Northcutt, 1986). Consequently we consider that the interpretation of Thomson is the most adequate interpretation available at present.

Denticles in the Narial Opening. We have commented that the presence of these denticles, in this genus at least, seems to rule out the possibility that the embayment in the wall of the naris carried a gland. The function of the denticles is more difficult to determine. Presumably they were covered with epidermis containing sensory cells of some kind, but beyond that we are unable to speculate, apart from noting that they would be ideally placed to monitor currents entering the nasal capsules.

FIG. 80. *Cladarosymblema narrienense*. Specimens all lightly acid-etched; SEMs. A, vertical section of small tusk, QMF33050, showing growth layers and strongly folded base. Scale: 1 mm. B, enlargement showing tubules different from those observed in other tusks in the collection; and therefore may not belong to the same taxon. Note, however, the difference between the two growth breaks; some tubules pass through the upper break but not the lower one. C, part of a vertical section through a deeply etched tooth, QMF33059, top to the left. Some of the tubules have broken during washing after the section had been etched, and are lying across the tubules that remain in place. D, enlargement of part of same to show that at least some of the growth banding results from multiple division of the tubules in the outer layer. E, enlargement of part of a section across a growth band, also of QMF31905. Note that the break consists of a layer of structureless material separating layers with tubules of different diameter and pattern. F, part of the same specimen showing closely spaced partitions within a main growth band.

RESPIRATION

Two main factors control the flow of water over the gills - the production of negative pressure (suction) in the buccal cavity by depression of the mandible and the gulars and lateral movement of the quadrate/mandible articulation, followed by the build-up of positive pressures in the buccal cavity by mouth closure, inwards movement of the quadrate/mandible articulation by contraction of the intermandibularis muscles, and the raising of the floor of the buccal cavity by contraction of the interhyoideus and intermandibularis muscles. Accompanying the build-up of positive buccal pressure is the production of negative pressures in the opercular chamber by movement of the opercular. The effectiveness of the pumping mechanisms can therefore be approached by examining the size and position of the submandibular muscle attachment areas, and the limits on the capacity of the opercular to move as reflected in the overlaps and muscle attachments of the opercular bones.

Muscles of Submandibular Region. In the absence of a ceratohyal, we are unable to comment on the size of the interhyoideus muscles, but the intermandibularis muscle attachments provide a good indication of the ability of those muscles to contract the buccal cavity. In *Latimeria chalumnae* both the anterior and posterior intermandibularis muscles are strongly developed (Millot & Anthony, 1958: vol. 2, fig. 28). Lauder (1980a) has shown that, primitively, the intermandibular musculature served to compress the buccal cavity rather than to take part in the depression of the mandible. In *Cladarosymblema* the posterior intermandibularis attachment surfaces are large, and are situated on the posterior half of the mandible. This suggests that they exercised a significant control on the extent of the lateral movement of the jaw articulation, as well as raising the floor of the buccal cavity during feeding and buccal pumping. The posterior intermandibularis muscles of *Latimeria* are attached to the anterior three-fifths of the mandible (Millot & Anthony, 1958: vol. 2, fig. 28); according to Jarvik (1963, fig. 20A) those of *Eusthenopteron* extend much further posteriorly, but the evidence for this interpretation is not clear. *Gogonassus* has an attachment of the intermandibularis extending posteriorly almost as far as the jaw articulation. This, taken in conjunction with the evidence from *Cladarosymblema* and *Eusthenopteron*, suggests that in osteolepiforms this may have been a normal feature. Assuming that the above interpretations are correct, we incline to the view that the

intermandibularis muscles played a more important role in buccal constriction in osteolepiforms than in *Latimeria*. The role of the hyomandibular in controlling the lateral movement of the jaw articulation is impossible to determine because, as indicated above we have no ceratohyal, and the ventral end of the hyomandibular appears to have been cartilaginous.

Egress of Water from the Gill Chamber. The posterior position of the intermandibularis muscles in osteolepiforms has another important consequence, viz. that egress of water from the gill chamber would have been anteroventrally restricted. The filament-bearing gills would therefore have been limited to a posterior and posteroventral position. This is consistent with the reconstruction of the gills in *Eusthenopteron* by Jarvik (1980: figs 109-110). In that genus, the anterior part of the buccal cavity contains a long sublingual rod that occupies the space containing the anterior ends of the gill arches in *Latimeria* and other primitive osteichthyans.

Opercular overlaps. The opercular is strongly overlapped anterodorsally by the lateral extrascapular, suggesting a severe restriction on its lateral movement. This overlap is larger than that of other osteolepiforms. However, as indicated in the descriptive section, the dorsal part of the opercular is inflected at a high angle, and lateral movement would require only a slight lift of the lateral extrascapular. Nevertheless, extensive lateral movement would be precluded. The subopercular 1 has a large surface where it was overlapped by the opercular, thus restricting its lateral movement unless the two bones moved in concert. At the same time, we note that these overlaps would have provided a stable form for the lateral and ventrolateral walls of the opercular chamber, thus maintaining the negative pressures generated by the limited lateral movement of the opercular and subopercular bones. We conclude that in comparison with the buccal pressure mechanism, the opercular mechanism provided only limited support for the respiratory water flow. This is not surprising, as Lauder (1985) has shown that in primitive fishes the negative pressures in the buccal cavity are five times those of the opercular cavity.

ACKNOWLEDGEMENTS

We wish to thank Mr and Mrs Muller of Springvale Station for assistance during field work. Dr Susan Turner, of the Queensland Museum, provided J.A.L. with the original material

collected by de Bretizel, and subsequently gave us access to maps that she had prepared during a collecting trip to the region. She also identified the microvertebrate material etched from our samples, and has continued to give support during the whole exercise. We thank Wiliam Ellis, Arvid Buskas and Laura Barwick for their assistance in the field. Dr Clinton Foster of the Australian Geological Survey Organisation has examined specimens from our samples for spores. Our Research Associate, Dr Peter Pridmore has consistently discussed matters of interpretation with us. Dr George Miklos and Prof. David Ride have discussed problems related to sensory reception. Dr. Ulf Borgen, of the Swedish Museum of Natural History, who has been studying the genus *Megalichthys* for some time, has freely made the results of his work available to us. Without this cooperation we would have been at a serious disadvantage. We thank Charles Schaff of the Museum of Comparative Zoology, Harvard, and John Maisey of the American Museum of Natural History for the loan of specimens of *Ectosteorhachis* for comparative study.

X-radiographs have been prepared by Wallace Ambrose of the Department of Prehistory, Research School of Pacific Studies, A.N.U.; and the Scanning Electron Micrographs have been prepared with the assistance of Mr Roger Heady, in the Electron Microscopy Unit of the A.N.U., and Dr Peter Pridmore. Interpretation of the thin sections of both scales and teeth has been assisted by Dr Tony Eggleton of the Geology Dept., A.N.U.

The acid preparation has proceeded over about ten years in the careful hands of Dr. Vicki Drapala, Ms Valerie Elder, Ms Melissa Fellows and Ms Claire Findlay. The beautiful mechanical preparation of the holotype, and preparation of latex and resin casts for study, is the work of Mr. L.A. Lindoe of the University of Alberta. Thin sections were made by Mr Norman Fraser and Mr John Vickers of the Geology Dept., Australian National University.

R.C.F.'s participation in the project was made possible by financial support from the Natural Sciences and Engineering Research Council of Canada, and by Study Leave from the University of Alberta in 1986, 1990 and 1994. K.S.W.C. and R.E.B. thank the Australian Research Council for financial support over many years. J.A.L. undertook the collecting trip and study of the de Bretizel material in 1985-6 while he held a Rothmans Fellowship in the Geology Dept., Australian National University.

LITERATURE CITED

- AHLBERG, P.E. 1991. A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society* 103: 241-287.
1992. The palaeoecology and evolutionary history of the porolepiform sarcopterygians. Pp. 71-90. In Mark-Kurik, E. (ed.), 'Fossil fishes as living animals'. (Academy of Sciences of Estonia: Tallinn).
- ANDREWS, S.M. 1973. Interrelationships of crossopterygians. Pp. 138-177. In Greenwood, P. H., Miles, R. S. & Patterson, C. (eds), 'Interrelationships of fishes'. (Linnean Society: London).
1982. The discovery of fossil fishes in Scotland up to 1845, with checklists of Agassiz's figured specimens. *Royal Scottish Museum Studies*: 1-82.
- ANDREWS, S.M. & WESTOLL, T.S. 1970a. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Transactions of the Royal Society of Edinburgh* 68(9): 207-329.
- 1970b. The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Transactions of the Royal Society of Edinburgh* 68(9): 391-489.
- BELLES-ISLES, M. 1992. The modes of swimming of sarcopterygians. Pp. 117-130. In Mark-Kurik, E. (ed.), 'Fossil fishes as living animals'. (Academy of Sciences of Estonia: Tallinn).
- BEMIS, W.E. & NORTHCUTT, R.G. 1992. Skin and blood vessels of the snout of the Australian lungfish, *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. *Acta Zoologica (Stockholm)* 73(2): 115-139.
- BIRKS, S.G. 1916. *Megalichthys*: a study incorporating the results of work on previously undescribed material. *Transactions of the Natural History Society of Northumberland, Durham, Newcastle (new series)* 4: 309-329.
- BJERRING, H.C. 1972. Morphological observations on the exoskeletal skull roof of an osteolepiform from the Carboniferous of Scotland. *Acta Zoologica* 53: 73-92.
- BORGEN, U. J. 1983. Homologizations of skull roofing bones between tetrapods and osteolepiform fishes. *Palaeontology* 26(4): 735-753.
1989. Cosmine resorption structures on three osteolepid jaws and their biological significance. *Lethaia* 22(4): 413-424.
1992. The function of the cosmine pore canal system. Pp. 141-150. In Mark-Kurik, E. (ed.) 'Fossil fishes as living animals'. (Academy of Sciences of Estonia: Tallinn).
- MS. Morphologic variation and classification of osteolepiform fishes. Based mainly on a study of the morphology of some osteolepid fishes. Unpublished manuscript.

- CAMPBELL, K.S.W. & BARWICK, R.E. 1982. A new species of the lungfish *Dipnorhynchus* from New South Wales. *Palaeontology* 25: 509-527.
1984. *Speonesydrion*, an Early Devonian dipnoan with primitive toothplates. *Palaeoichthyologica* 2: 1-48.
1987. Paleozoic lungfishes - a review. *Journal of Morphology Supplement* 1: 93-132.
- CHANG, M. 1982. The braincase of *Youngolepis*, a Lower Devonian crossopterygian from Yunnan, South-Western China. Unpublished PhD Thesis, Stockholm University.
1991. "Rhipidistians", dipnoans, and tetrapods. Pp. 3-28. In Schultze, H.-P. and Treub, L. (eds) *Origins of higher groups of tetrapods*. (Comstock Publishing Associates: Ithaca and London).
- CHANG, M. & SMITH, M.M. 1992. Is *Youngolepis* a porolepiform? *Journal of Vertebrate Paleontology* 12: 294-312.
- CHENG, H. 1989. On the tubuli in Devonian lungfishes. *Alcheringa* 13: 153-166.
- DE BEER, G. 1937. 'The development of the vertebrate skull'. (Oxford University Press: London).
- DE BRETIZEL, P.B. 1966. Le bassin de Drummond dans le géosynclinal de Tasman (Australie orientale). Doctoral Thesis, Fac. Sci., Univ. Lyons.
- EATON, T.H., Jr. 1939. The crossopterygian hyomandibular. *Journal of the Washington Academy of Science* 19: 109-117.
- FRICKE, H., REINICKE, O., HOFER, H. & NACHTIGALL, W. 1987. Locomotion of *Latimeria chalumnae* in its natural environment. *Nature* 329: 331-333.
- GRANDE, L. & BEMIS, W.E. 1991. Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae) with comments on the interrelationships of the Acipenseriformes. *Society of Vertebrate Paleontology, Memoir* 1: 1-121.
- GOODRICH, F.S. 1958. 'Studies on the structure and development of vertebrates'. 2 Vols. (Dover Publications: New York).
- GROSS, W. 1941. Über den Unterkiefer einige devonischer Crossopterygier. *Abhandlungen der preussische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 7: 1-51.
1956. Über crossopterygier und dipnoer aus dem baltischen oberdevon im Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems paläozoischer Agnathen und Fische. *Kungliga Svenska Vetenskapsakademiens Handlingar* 5: 1-140.
- HAY, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bulletin of the United States Geological Survey* 179: 1-868.
- HILL, D. 1957. Explanatory notes on the Springsure 4-mile Geological Series. *Note Series of the Bureau of Mineral Resources of Australia* 5: 1-19.
- JACK, R.L. & ETHERIDGE, R., Jr. 1892. The geology and palaeontology of Queensland and New Guinea. Publications of the Geological Survey of Queensland 92 (2 volumes).
- JANVIER, P. 1980. Osteolepid remains from the Devonian of the Middle East, with particular reference to the endoskeletal shoulder girdle. Pp. 223-254. In Panchen, A.L. (ed.), 'The terrestrial environment and the origin of land vertebrates'. (Academic Press: London).
1983. Les vertébrés Dévonien de la Nappe Supérieure d'Antalya. (Taurus Lycien occidental, Turquie). *Géologie Méditerranéenne* 10: 1-13.
- JARVIK, E. 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zoologiska Bidrag Från Uppsala* 21: 234-675.
1944. On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21: 1-48.
1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *Kungliga Svenska Vetenskapsakademiens Handlingar* 25: 1-301.
1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. *Kungliga Svenska Vetenskapsakademiens Handlingar* 5: 1-104.
1963. The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue. *Kungliga Svenska Vetenskapsakademiens Handlingar* 9: 1-74.
1966. Remarks on the structure of the snout in *Megalichthys* and certain other rhipidistid crossopterygians. *Arkiv för Zoologi* 19: 41-98.
1975. On the saccus endolymphaticus and adjacent structures in osteolepiforms, anurans and urodeles. *Colloque Internationaux Centre National de la Recherche Scientifique* 218: 191-211.
1980. 'Basic structure and evolution of vertebrates', 2 Vols. (Academic Press: London).
1985. Devonian osteolepiform fishes from East Greenland. *Meddelelser om Grønland, Geoscience* 13: 1-52.
- JONES, P.J., CAMPBELL, K.S.W. & ROBERTS, J. 1973. Correlation chart for the Carboniferous system of Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Commonwealth of Australia* 156A: 1-40.
- JORGENSEN, J.M., FLOCK, A. & WERSÄLL, J. 1972. The Lorenzian ampullae of *Polyodon spathula*. *Zeitschrift für Zellforschung und Microscopische Anatomie* 130: 362-377.
- KEMP, E.M., BALME, B.E., HELBY, R.J., KYLE, R.A., PLAYFORD, G. & PRICE, P.L. 1977. Carboniferous and Permian palynostratigraphy in Australia and Antarctica: a review. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics* 2: 177-208.

- KERR, T. 1955. The scales of modern lungfish. Proceedings of the Zoological Society of London 125: 335-345.
- LAUDER, G. 1980a. Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. Journal of Morphology 163: 283-317.
- 1980b. The role of the hyoid apparatus in the feeding mechanism of the coelacanth *Latimeria chalumnae*. Copeia 1980(1): 1-9.
1985. Functional morphology of the feeding mechanism in lower vertebrates. Fortschritte der Zoologie 30: 179-188.
- LONG, J.A. 1985a. A new osteolepidid fish from the Upper Devonian Gogo Formation, Western Australia. Records of the Western Australia Museum 12: 361-377.
- 1985b. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. Alcheringa 9: 1-22.
- 1985c. New information on the head and shoulder girdle of *Canowindra grossi* Thomson, from the Late Devonian Mandagery Sandstone, New South Wales. Records of the Australian Museum 37: 91-99.
1986. New ishnacanthid acanthodians from the Early Devonian of Australia, with comments on acanthodian relationships. Zoological Journal of the Linnean Society of London 87: 321-339.
1988. Late Devonian fishes from Gogo, Western Australia. National Geographic Research 4: 436-450.
1989. A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. Journal of Vertebrate Paleontology 9: 1-17.
- MEINKE, D.K. & THOMSON, K.S. 1983. The distribution and significance of enamel and enameloid in the dermal skeleton of osteolepiform rhipidistian fishes. Paleobiology 9: 138-149.
- MIALL, L.C. 1885. Description of the remains of *Megalichthys* in the Leeds Museum. The Leeds Philosophical and Literary Society: 1-15.
- MILLOT, J. & ANTHONY, J. 1958. Anatomie de *Latimeria chalumnae*. (3 Vols). (Centre National de la Recherche Scientifique: Paris).
- MOY-THOMAS, J.A. 1935. Notes on the types of fossil fishes in the Leeds City Museum. II. Acanthodii, Dipnoi, and Crossopterygii. Proceedings of the Leeds Philosophical Literary Society (Scientific Section) 3: 111-116.
- NORTHCUTT, R.G. 1986. Electrorception in non-telestost bony fishes. Pp. 257-285. In Bullock, T.H. & Heiligenberg, W. (eds), Electrorception. (Wiley: New York).
1987. Lungfish neural characters and their bearing on sarcopterygian phylogeny. Pp. 277-297. In Bemis, W. E., Burggren, W. W. & Kemp, N. E. (eds), 'Biology and evolution of lungfishes'. (Academic Press: New York).
- OLGERS, F. 1972. Geology of the Drummond Basin, Queensland. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics 132: 1-78.
- PANCHEN, A.L. 1967. The nostrils of choanate fishes and early tetrapods. Biological Reviews 42: 374-420.
- PANCHEN, A.L. & SMITHSON, T.R. 1987. Character diagnosis, fossils and the origin of tetrapods. Biological Reviews 62: 341-438.
- PLAYFORD, G. 1976. Plant microfossils from the Upper Devonian and Lower Carboniferous of the Canning Basin, Western Australia. Palaeontographica B, 158: 1-71.
1977. A Lower Carboniferous palynoflora from the Drummond Basin, east-central Queensland. Proceedings of the Royal Society of Queensland 88: 75-81.
1985. Palynology of the Australian Lower Carboniferous: a review. Compte Rendu, Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid, 1983, 4: 247-265.
- PRIDMORE, P.A. & BARWICK, R.E. 1993. Post-cranial morphologies of the Late Devonian dipnoans *Griphognathus* and *Chirodipterus* and locomotor implications. Memoir of the Association of Australasian Palaeontologists 15: 161-182.
- ROMER, A.S. 1937. The braincase of the Carboniferous crossopterygian *Megalichthys nitidus*. Bulletin of the Museum of Comparative Zoology 82: 1-73.
1941. Notes on the crossopterygian hyomandibular and braincase. Journal of Morphology 1: 141-160.
- ROSEN, D.E., FOREY, P.L., GARDINER, B.G. & PATTERSON, C. 1981. Lungfish, tetrapods, paleontology and plesiomorphy. Bulletin of the American Museum of Natural History 167: 159-276.
- SCHOLLE, P.A., BEBOUT, D.G. & MOORE, C.H. 1983. Carbonate depositional environments. American Association of Petroleum Geologists, Memoir 33: 1-704.
- SCHULTZE, H-P. 1969. Die Faltenzähne der rhipidistien Crossopterygier der Tetrapoden und die Actinopterygier Gattung *Lepisosteus*. Palaeontographica Italica 65: 63-137.
1974. Osteolepide rhipidistia (Pisces) aus dem Pennsylvanian von Illinois, USA. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 146: 29-50.
1987. Dipnoans as sarcopterygians. Journal of Morphology Supplement 1: 39-74.
1988. An osteolepidid rhipidistian in Upper Pennsylvanian deposits of Hamilton, Kansas. Kansas Geological Survey Guidebook Series 6: 181-183.
- SMITH, M.M. 1989. Distribution and variation in enamel structure in the oral teeth of sarcopterygians: its significance for the evolution of a protoprismatic enamel. Historical Biology 3: 97-126.

- SMITH, M.M., HOBDELL, M.H. & MILLER, W.A. 1972. The structure of the scales of *Latimeria chalumnae*. Journal of the Zoological Society of London 167: 501-509.
- SMITHSON, T.R. & THOMSON, K.S. 1982. The hyomandibular of *Eusthenopteron foordi* Whiteaves (Pisces Crossopterygii) and the early evolution of the tetrapod stapes. Zoological Journal of the Linnean Society 74: 93-103.
- THOMSON, K.S. 1964a. Revised generic diagnoses of the fossil fishes *Megalichthys* and *Ectosteorhachis* (family Osteolepidae). Bulletin of the Museum of Comparative Zoology 131: 283-311.
- 1964b. The comparative anatomy of the snout in rhipidistian fishes. Bulletin of the Museum of Comparative Zoology 131: 313-357.
1965. The endocranium and associated structures in the Middle Devonian rhipidistian fish *Osteolepis*. Proceedings of the Linnean Society of London 176: 181-195.
1967. Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. Zoological Journal of the Linnean Society 46: 223-253.
1969. The biology of the lobe-finned fishes. Biological Reviews 44: 91-154.
1975. On the biology of cosmine. Bulletin of the Peabody Museum of Natural History 40: 1-59.
- THOMSON, K.S. & RACKOFF, J.S. 1974. The shoulder girdle of the Permian rhipidistian fish *Ectosteorhachis nitidus* Cope: structure and possible function. Journal of Paleontology 48: 170-179.
- THOMSON, K.S. & VAUGHN, P.P. 1968. Vertebral structure in Rhipidistia (Osteichthyes, Crossopterygii) with description of a new Permian genus. Postilla Peabody Museum Yale University 127: 1-19.
- TURNER, S. 1993. Early Carboniferous microvertebrates from the Narrien Range, central Queensland. Pp. 289-304. Memoir of the Association of Australasian Palaeontologists 15: 289-304.
- VINE, R.R. & DOUTCH, H.F. 1972. Explanatory notes on the Galilee (Queensland) 1:250000 Geological Series, Sheet SF/55-10. Bureau of Mineral Resources Geology and Geophysics:1-20.
- VOROB'JEVA, E.I. 1962. Rhizodontid crossopterygians of the Main Devonian Field in the USSR. Trudy Paleontologicheskogo Instituta. Akademiya Nauk SSSR 94: 1-139. [In Russian].
1977. Morphology and specific features of the evolution of crossopterygian fishes. Instituta. Akademiya Nauk SSSR 163: 1-240. [In Russian].
- WARREN, A.A. & DAVEY, L. 1992. Folded teeth in temnospondyls - a preliminary study. Alcheringa 16(2): 107-132.
- WATSON, D.M.S. 1926. The evolution and origin of the Amphibia. Philosophical Transactions of the Royal Society of London 204: 189-257.
- WEBB, P.A. 1982. Locomotor patterns in the evolution of actinopterygian fishes. American Zoologist 22: 329-342.
- WESTOLL, T.S. 1936. On the structures of the dermal ethmoid shield of *Osteolepis*. Geological Magazine 73: 157-171.
1937. On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. Geological Magazine 74: 507-524.
1940. New Scottish material of *Eusthenopteron*. Geological Magazine 77: 65-73.
1943. The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. Proceedings of the Royal Society of London (13), 131: 393-414.
- WHITE, M.E. 1972. Plant fossils from the Drummond Basin, Queensland. Pp. 73-78. In Olgers, F., Geology of the Drummond Basin, Queensland. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics 132: 1-78.
- YOUNG, G.C. 1986. The relationships of placoderm fishes. Zoological Journal of the Linnean Society 88: 1-57.
- YOUNG, G.C., LONG, J.A. & RITCHIE, A. 1992. Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. Records of the Australian Museum, Supplement 14: 1-77.

*NOTE ADDED IN PROOF

Dr Oleg Lebedev has drawn our attention to a couple of points in our interpretation where details of a new Russian osteolepiform, described in the proceedings of the Miguasha Symposium on early vertebrates, indicate that we may be in error.

Firstly the bone described and figured as a urohyal is not sufficiently compressed and does not have the anterior articulation surfaces of that bone. Instead it is more likely to be a basal radial from the second dorsal or anal fin (see Jarvik, 1980; fig. 99). This is an attractive interpretation.

Secondly the anterior edge of the parasphenoid may have been placed in a too posterior position on our Fig 20A. In the Russian specimen the anterior edge is approximately along the posteromesial edge of the vomers. Our best preserved specimen has a clear boundary in the position we have indicated, and the more anterior boundary near the edge of the vomers is not so well preserved. Hence, whereas we acknowledge the possibility that we are in error, our opinion on the issue remains ambiguous.

ADDENDUM

The specimens extracted from the limestone block collected by de Bretizel, and said to be from the Telemon Formation, have been catalogued as QMF26522. They have many features in common with *Cladarosymblema narrienense*, but in view of their unknown provenance, and the record by Turner (pers. comm.) of fish remains in situ in carbonates of the Telemon Formation within the Narrien Anticline, we have decided to keep the material separate. The following notes concentrate on differences from the type material of *C. narrienense*. Some of the specimens have been illustrated in Fig. 12.

The single fragment of the ethmoid shield has a large median postrostral, posterior nasals that indent the outline of the parietals, and a patch of sensory pores lies on the posterior nasal as in *C. narrienense*. The lateral margins of the parietals converge posteriorly unlike those of *C. narrienense*.

One lachrymal is available. It is one third as high as long, and in dorsal view is seen to be flexed inwards near its anterior end. Its posterior end is acute and it has a distinctive overlap arrangement with the jugal. This shape and overlap pattern does not match the anterior edge of the jugal of *C. narrienense*, which is much more upright. The ventral edge has cosmine to its margin, and a slight furrow of irregular depth internally, into which the maxilla fits. The notch for the articulation of the anterior process of the maxilla is not pronounced. The anterodorsal edge also has cosmine to its margins and a distinctive groove and peg for articulation with the lateral rostral. Anterior to this peg and immediately dorsal to the lateral line canal is a complementary articulatory socket. The edge forming the orbital margin is very short and is bevelled as is normal. According to Borgen (MS), in *M. hibberti* the suture between the lachrymal and the jugal does not reach the orbit, implying that the jugal forms the entire ventral margin of the orbit. This is clearly not the case in this species. The infraorbital lateral line canal runs close to and parallel with

the ventral margin, opening to the exterior via large pores some of which are almost on the bone margin. A number of offshoots run up from the main canal to open on the anterior part of the bone.

A relatively complete isolated lateral extrascapular is known. The bone is subtriangular in outline, but with all the edges slightly curved. The anterior margin bears a narrow overlapped surface, and its lateral edge is finished. The mesial edge is finished and rather thin, showing that it overlapped the median extrascapular. A 7 mm long, flexed, longitudinal pitline runs down the axis of the bone, and a second much longer line loops around this one, presumably having run onto the bone from the median extrascapular.

About half of a maxilla is well preserved. It has a ridge like that of *C. narrienense* supporting the tooth row on its internal surface, but it lacks protuberances on its dorsal edge and the overlapped edge is more extensive. As described above, the anterior process is large and has a folded dorsal tip which probably formed the posterior edge of the choana as in *Gogonasus andrewsae*.

Only a small fragment of a mandible is available; it does not provide an adequate basis for comparison.

A well-preserved opercular and a median gular match those of *C. narrienense* except that the median gular has well-developed pitlines. The opercular even has the small patch of sensory pores in its anterodorsal corner. The scales of the two are entirely comparable.

Two isolated specimens that may be subopercular 1 have been recovered, but they are very long and have overlap patterns that cannot be reconciled satisfactorily with that identification.

Consequently, we have concluded that this species is closely related to *C. narrienense*, but in view of the small differences in the shapes of the parietal and the mandible, and the failure of the lacrymal to fit the jugal of *C. narrienense*, it is not possible to say that they are conspecific.

A NEW SPECIES OF *PARTHENOPE* (CRUSTACEA: DECAPODA: PARTHENOPIDAE)
FROM DEEP-WATER OFF NORTHERN QUEENSLAND

JOHN S. GARTH & PETER J.F. DAVIE

Garth, J.S. & Davie, P.J.F. 1994 06 01: A new species of *Parthenope* (Crustacea: Decapoda: Parthenopidae) from deep-water off northern Queensland. *Memoirs of the Queensland Museum* 38(1): 223-227. Brisbane. ISSN 0079-8835.

A new species, *Parthenope* (*Platylambrus*) *cidaris*, has been collected using an epibenthic sledge from 685m in the waters off northeastern Queensland. It belongs to the *P. (P.) stellata* species group, and is separated from the known species by differences in carapace granulation and spination, carapace regional differentiation, and some claw characters. Photographs of the holotypes of *P. stellata*, *P. complanata*, and *P. lacunosa*, all described by Rathbun (1906) are presented for comparison. □ *Crustacea, Decapoda, Brachyura, Parthenopidae, Parthenope, Platylambrus, new species, deepwater, Queensland.*

John S. Garth (deceased), Allan Hancock Foundation, Los Angeles, California, USA 90089-0371; Peter J.F. Davie, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 21 March 1995.

In September 1988 the R.V. *Franklin*, under the direction of Professor Michel Pichon, carried out an exploratory cruise in the east Australian bathyal zone. This cruise, known as 'CIDARIS II' was one of a series of three conducted as part of the research project 'The deep-water benthos off the Great Barrier Reef Shelf and adjacent Coral Sea'. The CIDARIS cruises employed beam trawls, Charcot dredges and epibenthic sledges on the continental slope of the Great Barrier Reef, and also in the Queensland basin.

Along the east Australian coast, deep-water crabs have been most recently studied by Griffin & Brown (1976), Griffin & Tranter (1986a, b), Davie and Short (1989). A large paper recording many new species and records from northeastern Australia and the Coral Sea is currently in preparation (Davie & Richer de Forges, in prep.).

The present *Parthenope* species belongs to a group in the subgenus *Platylambrus* found in deep-water in the eastern central Pacific, discussed and described by Garth (1993), viz. *P. stellata* Rathbun, 1906, *P. complanata* Rathbun, 1906, *P. lacunosa* Rathbun, 1906, *P. mironovi* (Zarenkov, 1990), *P. poupini* Garth, 1993, and *P. allisoni* Garth, 1993. Of these it is most closely allied to *P. stellata* and *P. poupini*, but it differs from them sufficiently to warrant specific separation.

Abbreviations: mm, millimetres; QMW, Queensland Museum, Brisbane; USNM, Smithsonian Institution, United States National Museum, Washington.

SYSTEMATICS

Parthenope (*Platylambrus*) *cidaris* sp. nov.
(Figs 1, 2A)

MATERIAL EXAMINED

HOLOTYPE: QMW16086, ♀, CIDARIS II, Stn 23.4, 14°52'S, 145°46'E, 9.9.1988, 685m, epibenthic sledge.

DESCRIPTION

Measurements (in mm): length 36.8, width 52.8, length of major (right) cheliped 84.0, of chela 43.8, of dactyl 18.8, height of palm 19.3.

Carapace triangular, broader than long, length 1.43 times width, deeply channelled, microscopically eroded and pitted, a few larger tubercles at ends of ridges. Front slender, tip rounded, sides gently sloping toward slightly advanced inner orbital margin; thickened ridge extending backward onto protogastric region. Major elevations disposed as follows: proto- and mesogastric separated widely from cardiac-intestinal, these separated widely from metabranchial and branchial. Branchial ridge diagonally directed, divided by row of pits into larger posterior and smaller anterior ridge. Anterolateral margins arcuate, dentate, teeth denticulate, those on hepatic and anterior branchial portions larger. Last anterolateral tooth spatulate; backward-pointing tubercle at end of branchial and metabranchial ridges.

Merus of third maxilliped flaring anterolaterally, margin crescent-shaped, crossed by median ridge.

Chelipeds grossly disproportionate, right largest; left, although perfectly formed, feeble and perhaps regenerated. Merus trigonal, spinous-

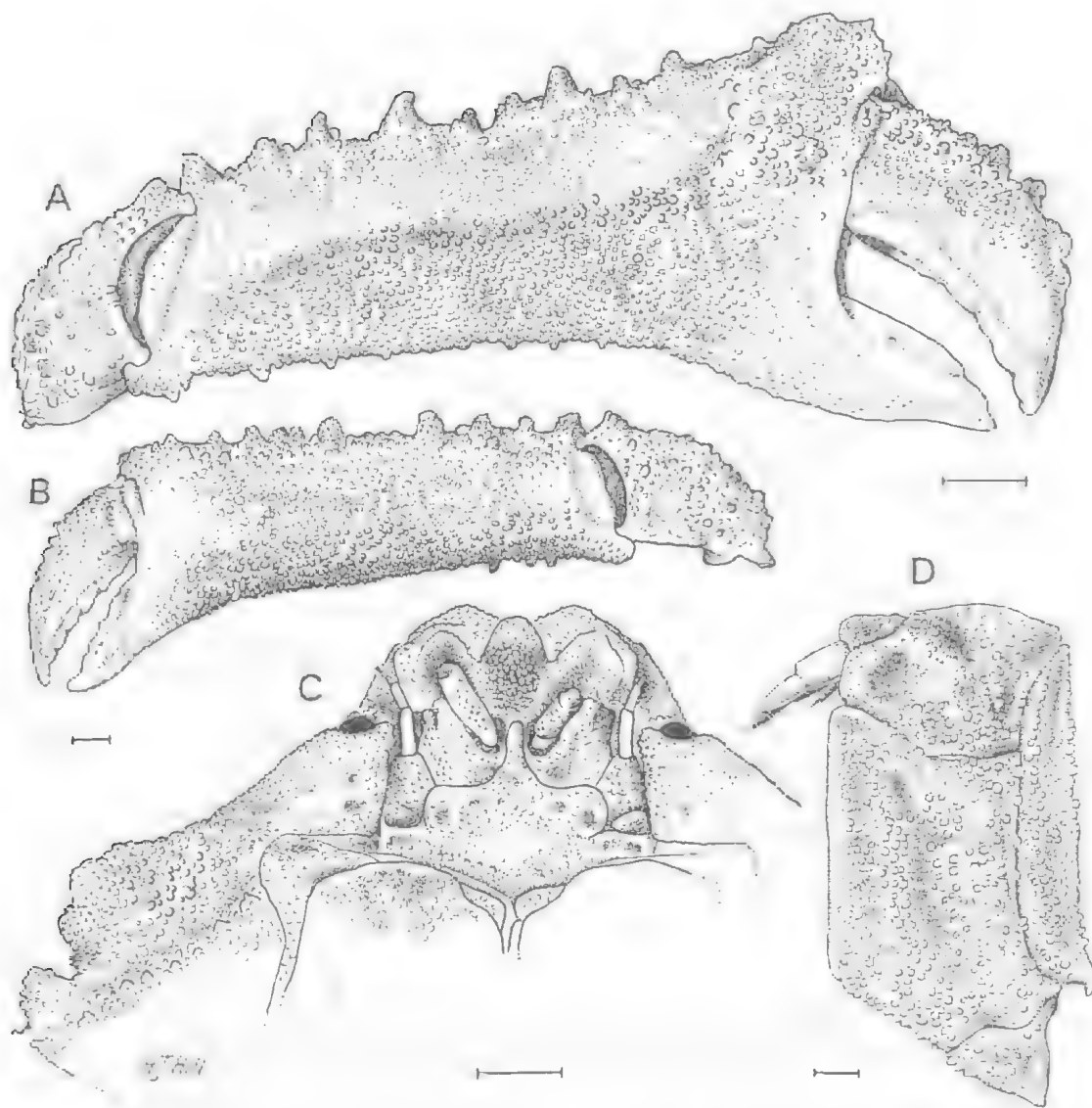


FIG. 1. A-D, *Parthenope cidaris* sp. nov., holotype ♀. A, right chela. B, left chela. C, frontal view. D, third maxilliped.

margined, carpus likewise, propodus gradually increasing in width distally, large spines on crest, row of spines turning upward on inner margin. Fingers incurving, gaping, brown colouring extending to tips.

Walking legs slender, decreasing regularly in length from first to last; meri spinous above and below; carpi with two triangular flanges; propodi spinous basally; dactyli smooth, curved, felled.

Female abdomen six-segmented, tuberculate.

REMARKS

As compared to the holotype of *P. (P.) stellata* Rathbun 1906, the *P. cidaris* female lacks the overall paving with stellate granules that suggested to Rathbun the name 'stellata'. The vast proportion of the granules are single, only a few tending to merge, let alone form stars. The single tubercles that in *P. stellata* top the gastric, cardiac, and branchial regions are lacking in *P. cidaris*, although some larger tubercles occur posteriorly. The branchial ridge is more promi-

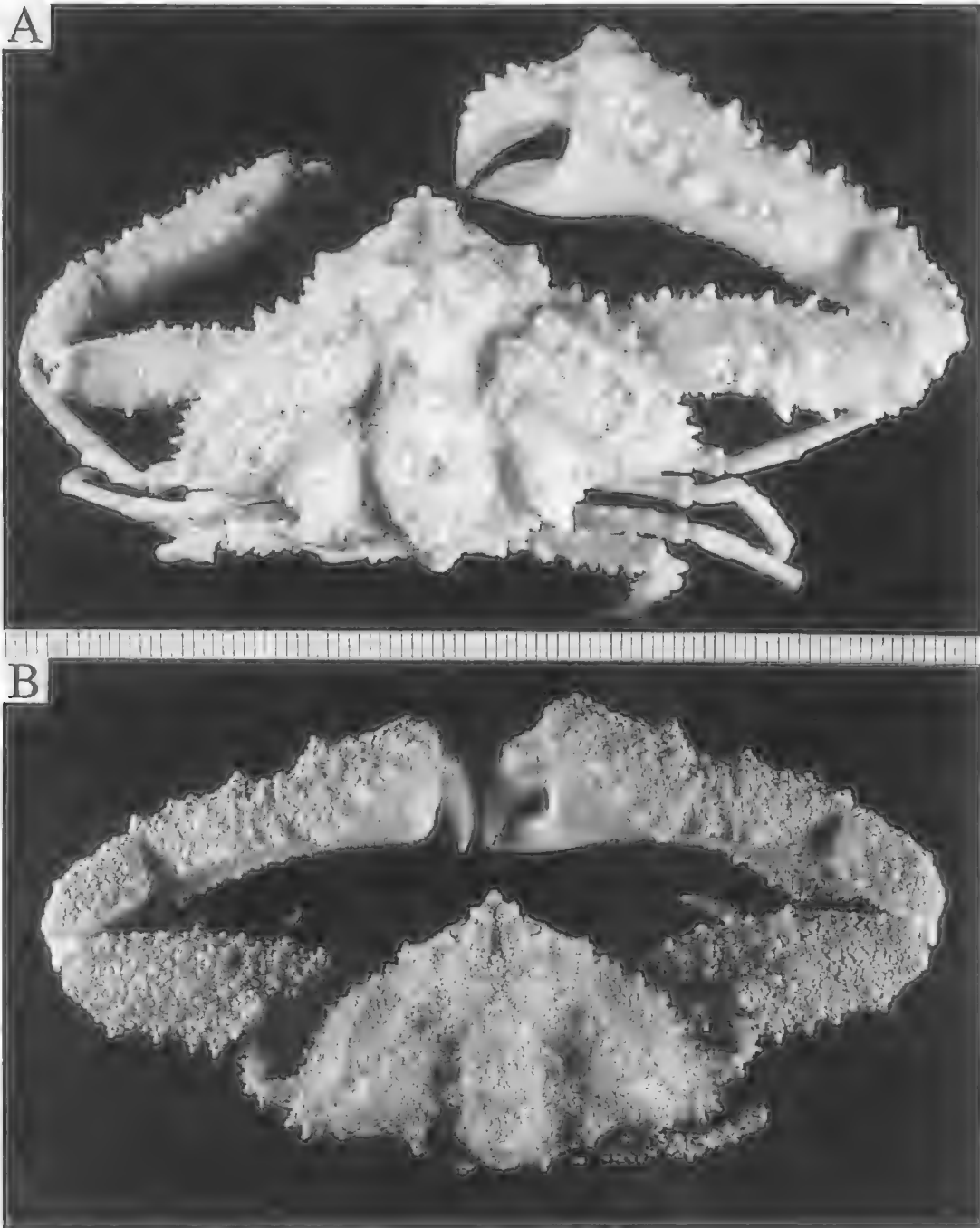


FIG. 2. A, *Parthenope cidaris* sp. nov., holotype ♀. B, *P. stellata* Rathbun, 1906, holotype, USNM.

nent and swollen, and the furrows separating it from the metabranchial and cardiac regions are deeper. The last spine of the lateral ridge is spatulate, as is the spine internal to it, on the left side,

at least. The chelipeds, especially their propodi, are more prominently trigonal in cross-section, the intervening flat surfaces almost smooth. The outer surfaces of the hands, both major and minor,

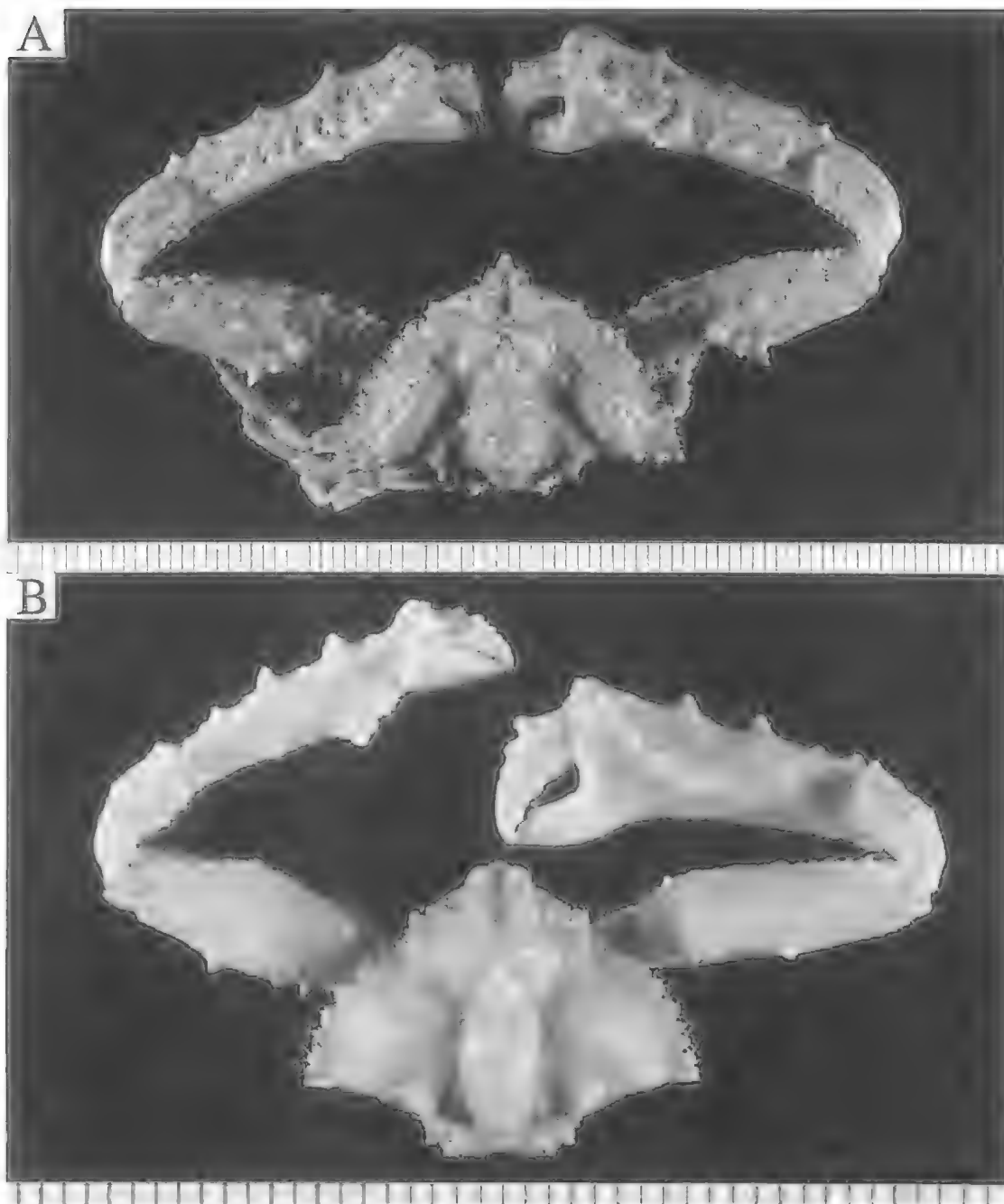


FIG. 3. A, *P. lacunosa* Rathbun, 1906, holotype, USNM. B, *P. complanata* Rathbun, 1906, holotype, USNM.

are smoother, except for a median tuberculate ridge on the major manus.

As compared to the holotype of *Parthenope* (*P.*) *poupini* Garth, 1993, from French Polynesia, the *P. cidaris* female is much broader, the elevations of the carapace more prominent, the spines

of the anterolateral margins longer and sharper. The ridges, which in *P. poupini* tend to fuse, retain their distinct tuberculation in *P. cidaris*.

Garth (1993) previously recognised that *P. stellata* Rathbun, 1906 (Fig. 2B), as well as its named varieties, *P. stellata complanata* Rathbun,

1906 (Fig. 3B), and *P. stellata lacunosa* Rathbun, 1906 (Fig. 3A), all must have full species rank. As part of this study we re-examined the holotypes of all three taxa, and while *P. cidaris* is most clearly allied with *P. stellata*, it is useful to publish new photographs of the holotypes of all species. We believe that *Parthenope* (*P.*) *cidaris*, while undoubtedly belonging to the same species-group as *P. stellata* is also sufficiently distinct to deserve specific rank.

ACKNOWLEDGEMENTS

We are very grateful to Dr Ray Manning of the USNM for the loan of type specimens. Our thanks also to John Short for his photographic skills, and to Alison Hill for her excellent illustrations.

LITERATURE CITED

- DAVIE, P.J.F. & RICHER DE FORGES, B. (In prep.) Deep-water Brachyura (Crustacea: Decapoda) from northern Australia. The Results of the Cidaris I-III and Soela cruises.
- DAVIE, P. & SHORT, J. 1989. Deep-water Brachyura (Crustacea: Decapoda) from southern Queensland, Australia: with descriptions of four new species. *Memoirs of the Queensland Museum* 27(2): 157-87.
- GARTH, J.S. 1993. Some deep-water Parthenopidae (Crustacea, Brachyura) from French Polynesia and nearby eastern Pacific Ridges and Seamounts. *Bulletin du Muséum National d'Histoire Naturelle*, 4th ser., 14, sect. A (3-4)[1992]: 781-795.
- GRIFFIN, D.J.G. & BROWN, D.E. 1976. Deepwater Decapod Crustacea from Eastern Australia: Brachyuran Crabs. *Records of the Australian Museum* 30: 248-271.
- GRIFFIN, D.J.G. & TRANTER, H.A. 1986a. The Decapoda Brachyura of the SIBOGA Expedition. Part VIII: Majidae. *Siboga Expedition Monograph* 39 (C4), 148: 1-335.
- 1986b. Some Majid Spider crabs from the deep Indo-west Pacific. *Records of the Australian Museum* 38: 351-371.
- RATHBUN, M.J. 1906. The Brachyura and Macrura of the Hawaiian Islands. *Bulletin of the United States Fisheries Commission* 23 (1903): 827-30.
- ZARENKOV, N. A., 1990. Decapods (Stenopodidea, Brachyura, Anomura) of the Nazca and Sala-y-Gomez underwater ridges. [in Russian]. *Transactions of the P.P. Shirshov Institute of Oceanology. Academy of Sciences of the USSR* 124: 218-244.

FAUNAL SURVEY OF NEW ENGLAND. IV. THE FROGS

HAROLD HEATWOLE, JOHN de BAVAY, PAUL WEBBER AND GRAHAME WEBB

Heatwole, H., de Bavay, J., Webber, P. and Webb, G. 1995 06 01: Faunal survey of New England. IV. The frogs. *Memoirs of the Queensland Museum* 38(1): 229-249. Brisbane. ISSN 0079-8835.

Distributions and habitats of 46 species of frogs, representing 13 genera within two families are documented in a faunal survey of the New England Region, northern New South Wales. Two species; *Litoria castanea* and *Litoria piperata* are endemic to the region. Twelve species are eurytopic, most frogs are from moist habitats which have distributions along the east coast and onto the Great Dividing Range, and these are restricted to the eastern New England region. Those frogs species known from the western arid plains are restricted to the western part of the New England region. □ *New England, frogs, fauna survey, distribution, habitat.*

Harold Heatwole, North Carolina State University, Department of Zoology, College of Agriculture and Life Sciences, Raleigh NC 27695-7617, USA; John de Bavay, Department of Zoology, University of New England, Armidale NSW 2351, Australia; Paul Webber, Webber & Associates, Middle Farm Road, Armidale NSW 2350, Australia; Grahame Webb, Wildlife Management International Pty Ltd, PO Box 38151, Winnellie NT 0821, Australia; 06 April 1995.

In 1966 the New England Faunal Survey was initiated. This faunal survey fulfils the following functions; (1) It catalogues the species of the area and provides clues for their identification, (2) presents information on local distribution, (3) allows faunal assessment of localities providing a data set from which baseline environmental management policies can be derived, and (4) highlights ecological similarities and differences between component species and generates hypotheses as to factors influencing the geographic distribution of species allowing temporal changes to be monitored and recorded.

Taxa covered by the survey have depended on the number and enthusiasm of students and staff of the University of New England and has reflected their interests towards particular taxonomic groups. Many groups have not received any attention due to a lack of appropriate specialists: participation of interested qualified persons is most welcome.

Three parts of the survey have been published. The first (Heatwole & Simpson, 1986) was a general account of the region's geography, drainage systems, topography, climate, vegetation, geology and soils, and was designed as a background for later papers dealing with specific taxa. The second part (Simpson & Stanisic, 1986) treated the snails and slugs of the region and the third (Ford & McFarland, 1991) dealt with birds.

The present paper provides a species list of the frogs, a distributional map for each species, and an interpretation of the biogeography of the region based on this taxon. It is expected that two

further herpetofaunal papers will appear in the series, one on lizards, and one on snakes and freshwater tortoises.

METHODS

Methods related to this faunal survey have been described in previous papers of this series and are here briefly summarised. The initial data base comprised opportunistic collecting, road kills, a small previous collection in the Department of Zoology of the University of New England, specimens brought in by the public, and the collections of the Australian Museum, Sydney. Additional data were obtained from the collections of the Queensland Museum, Brisbane and the Museum of Victoria, Melbourne. Material used in this study spans a period from early 20th century to 1990. Specimens were catalogued and localities of their provenance plotted on gridded outline maps of the area. Such maps form the basis for Figs 6-46. Preserved specimens contributing to the initial data base are represented by solid symbols, those from other sources by open circles. When major distributional outlines had emerged, special collecting trips were made to specific areas to fill in gaps. There are many details yet remaining, and rare species may be treated inadequately. However, it was deemed that most patterns were sufficiently clear to warrant presentation of the results.

Previous papers in this series have employed the Australian Biogeographical Integration Grid System (ABIGS) (Brooks, 1977) using squares

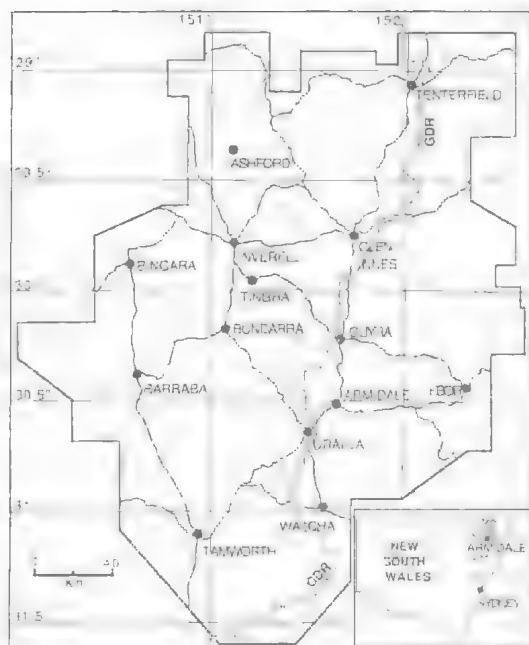


FIG. 1. Collecting grid and study area within New South Wales indicating main towns, connecting roads and the Great Dividing Range (GDR). Inset shows the location of the study area in New South Wales.

formed from 5' or 10' units of latitude and longitude, superimposed on a like-scale map of the region. The system recorded distribution as a set of grid localities. The present paper uses latitude and longitude to provide individual site records for each species. In both systems frog distributions are superimposed on a stylised outline of the 1968 New England Electorate, originally selected as a convenient unit for study (Fig. 1). Distributional maps presented here have been computer-generated using the Environmental Resources Mapping System (ERMS) devised by the National Parks and Wildlife Service of New South Wales, as were maps of elevation, rainfall and vegetation (Figs 3-5). The temperature map (Fig. 2) is from an 'Atlas of New England' (Lea et al., 1977). Distribution of each species was compared to these maps of environmental parameters.

The project was carried out under a succession of permits from the National Parks and Wildlife Service and approvals by the Animal Welfare Committee of the University of New England. Preserved specimens were donated to public Aus-

tralian research museums, primarily the Australian Museum in Sydney.

ANNOTATED SPECIES LIST

In all, 46 species from 13 genera in two families are represented in the area. The family Myobatrachidae had 26 species in 11 genera and the family Hylidae had 20 species in 2 genera (2 in *Cyclorana* and 18 in *Litoria*).

The following list gives general information about each species, including its overall geographic range and its distribution in the New England area. Anecdotal habitat data arising from our collections and field notes are summarised. For further information, the reader can consult Barker & Grigg (1977), Cogger (1992), Tyler (1992) and the catalogue by Cogger et al. (1983). The latter provides an annotated bibliography that serves as a useful guide to the literature on each species. Some of the following information is taken from those sources.

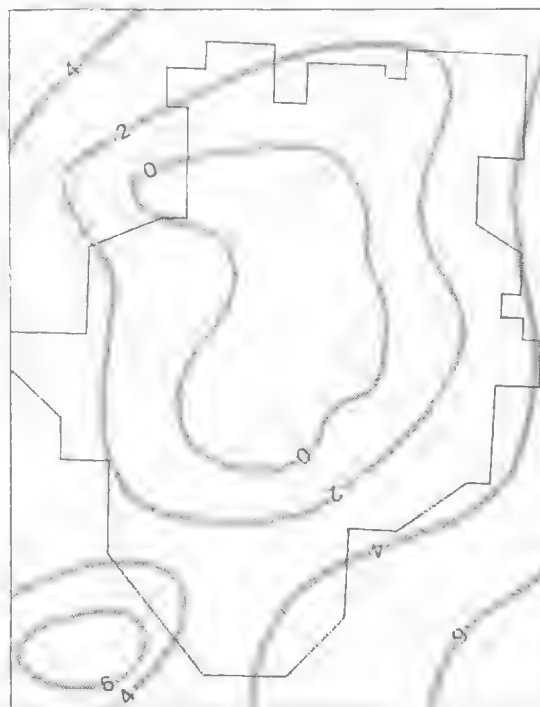


FIG. 2. Mean daily minimum isotherms (°C) across the New England region for July, superimposed on the study area. Modified from Lea et al. (1977).

FAMILY HYLIDAE

Superb Collared Frog *Cycloranus brevipes*
(Peters, 1871) (Fig. 6)

HABITAT: Grassy woodland; drier coastal areas and ranges.

RANGE: NE and E Australia only (Cogger, 1992).

NEW ENGLAND RANGE: There are three, possibly four, records of this species, all from the northern part of the study area. Two of these records AMR36867 and AMR37213 were registered in the Australian Museum as *C. cultripes*. The former has now been identified as *C. brevipes*, the latter cannot be located but since the locality of this specimen coincides with that of one of the specimens of *C. brevipes* there is little doubt that it, too, belongs to that species. Arranged along a line joining Yetman and Tenterfield these records represent an extension of previously known range for *C. brevipes*.

Water-holding Frog *Cyclorana platycephala*
(Günther 1873) (Fig. 6)

HABITAT: The arid and semi-arid areas of the Australian interior.

RANGE: This species ranges in a broad band across arid Australia from the west coast of Western Australia through southern Northern Territory, northern South Australia to the western districts of Queensland and New South Wales.

NEW ENGLAND RANGE: The specimens recorded were taken near Gunnedah, outside the study area but which lies within the wider New England region defined by Lea et al. (1977). It is included here because the record may represent the eastern limit of its range.

Green and Gold Bell Frog *Litoria aurea* (Lesson, 1829) (Fig 7)

HABITAT: An aquatic species inhabiting reed beds in or edging natural or artificial permanent waters.

RANGE: Coastal, northern N.S.W. to southeastern Victoria. Extends west of the Great Dividing Range in southern N.S.W.

NEW ENGLAND RANGE: Two records near Armidale, one at Ebor.

Litoria barringtonensis (Copland, 1957) (Fig. 18.)

RANGE: Coastal ranges north of the Hunter River (M. Mahony, pers. comm.) to the Border Ranges.

NEW ENGLAND RANGE: All records are from or near the eastern boundary of the study area, in high, wet forest (elevation 400-1200m; rainfall 1100-1500mm) along the edge of the escarpment which represents the western limits of the species and of the coastal area.

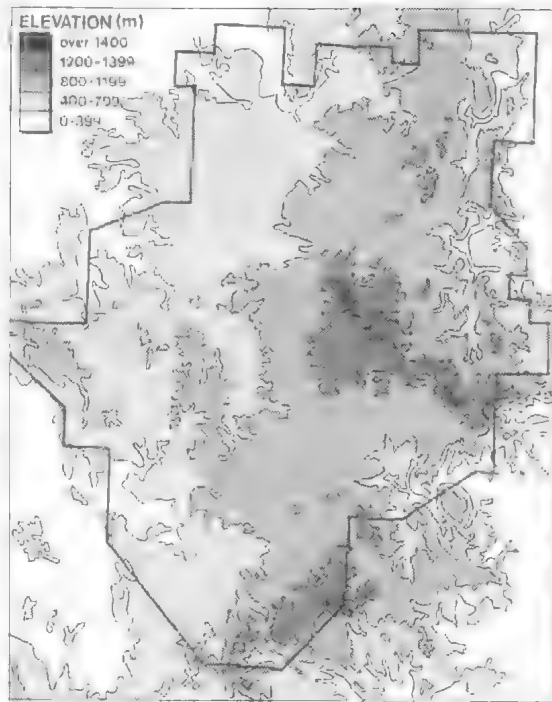


FIG. 3. Elevations of the study area. Adapted from a computer-generated map incorporating recent data provided by the Armidale branch of the National Parks and Wildlife Service of New South Wales.

COMMENT: These records were originally considered to represent *L. phyllochroa*. Currently there is uncertainty concerning the relationships of *L. phyllochroa*, *L. barringtonensis*, *L. pearsoniana* and *L. piperata*, all members of the *L. phyllochroa* complex. The identification adopted here was provided by M. Mahony, University of Newcastle, from adult specimens. However, it should be noted that the map records for this designation include tadpoles of a generally *L. phyllochroa* conformation and the possibility exists that they may represent *L. pearsoniana* or *L. barringtonensis*.

Booroolong Frog *Litoria booroolongensis*
(Moore, 1961) (Fig. 8)

HABITAT: Nearly always associated with flowing water, typically the rocky, mountain streams of the Great Dividing Range.

RANGE: Mainly the ranges along the Great Dividing Range from Queensland to the Victorian-New South Wales border but extending westwards into lower rainfall areas.

NEW ENGLAND RANGE: Widespread in the study area, the most easterly records lying outside the study area, 22.5km northwest of Dundurrabin. The most

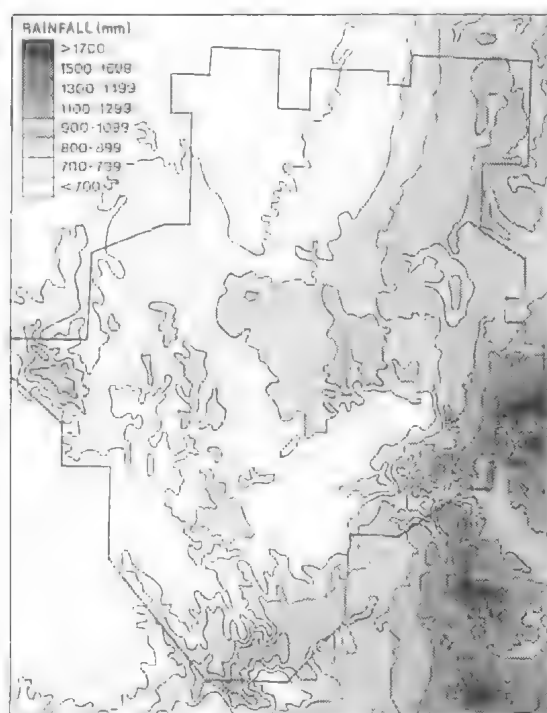


FIG. 4. Mean annual rainfall of the study area. Adapted from a computer-generated map incorporating recent study data by the Armidale branch of the National Parks and Wildlife Service of New South Wales.

northerly is a dubious record from Boonoo-Boonoo 22.5km north of Tenterfield, but otherwise from the Severn River, 11km southeast of Emmaville. The most southerly record is from 5km south west of Nundle. The absence of records from the northwestern and southwestern part of the study area is attributed to these being lower and drier areas.

Table 1 shows that distribution of *L. booroolongensis* coincides with a wide range of July minimum temperatures and with the drier end of the spectrum for rainfall and system of vegetation. There is a strong correlation with elevation both inside and outside of the study area, 65% of site records being above 800m. It is clear that distribution of this frog correlates with a particular habitat, itself dependent on relief.

Green Tree Frog *Litoria caerulea* (White, 1790) (Fig. 9)

RANGE: Widespread, coastal to dry interior; south-eastern N.S.W., all of Queensland and the monsoonal parts of northern Australia.

NEW ENGLAND RANGE: A minor part of the total range. Occurs throughout the region but is much less common on the Tablelands than in the coastal areas. It

seems likely that its New England distribution may owe much to human activity.

New England Swamp Frog *Litoria castanea* (Steindachner, 1867) (Fig. 7)

HABITAT: Associated with ponds, large permanent pools, small lakes and quiet streams all characterised by an abundant marginal growth of bullrushes and other vegetation. Found among reeds, in the water and under logs.

RANGE: This is an isolated population confined to the New England Tablelands, and known only from the central area of New England on either side of the Great Dividing Range, where it occupies mainly the headwaters of the westerly flowing Booroolong Creek and to a lesser extent those of the easterly flowing Anne and Sarah Rivers. Near Armidale, it has been recorded from Commissioners Waters, a tributary of the easterly flowing Gara River. No sightings in the wild have been reported since 1972 (Courtice & Grigg, 1975). Fears must be held for its survival. However, R. Hayworth of the University of New England Department of Geography and Planning reports collecting a specimen from dumped soil on a vacant lot actually within Armidale in 1991. Presumably it had been accidentally transported in the load of soil. Unfortunately, the identity of the specimen, which was released, cannot be confirmed.

Red-eyed Tree Frog *Litoria chloris* (Boulenger, 1893) (Fig. 10)

HABITAT: Coastal rainforest, wet sclerophyll forests and grassy flood plains.

RANGE: Coast and adjacent eastern Australia from Gosford, N.S.W. to central eastern Queensland (Cogger, 1992).

NEW ENGLAND RANGE: There are only two records, both from the eastern boundary of the study area, i.e., the western boundary of the coastal rain forest. The New England Tableland marks the western limits of this essentially coastal species.

Keferstein's Tree Frog, Bleating Tree Frog *Litoria dentata* (Keferstein, 1868) (Fig. 11)

HABITAT: Commonly associated with coastal lagoons and swamps, especially *Melaleuca* swamps behind coastal sandhills (Cogger, 1975).

RANGE: Comprises the coastal plain and adjacent mountains of eastern Australia from Jervis Bay north as far as the Maryborough district of Queensland. Moore (1961) recorded it from Palamallawa, between Warialda and Moree, as the only record west of the mountains. This record is further west than any from the present study.

NEW ENGLAND RANGE: Predominantly eastern. Of 11 records from the study area, three are west of Great Dividing Range. The Palamallawa record of

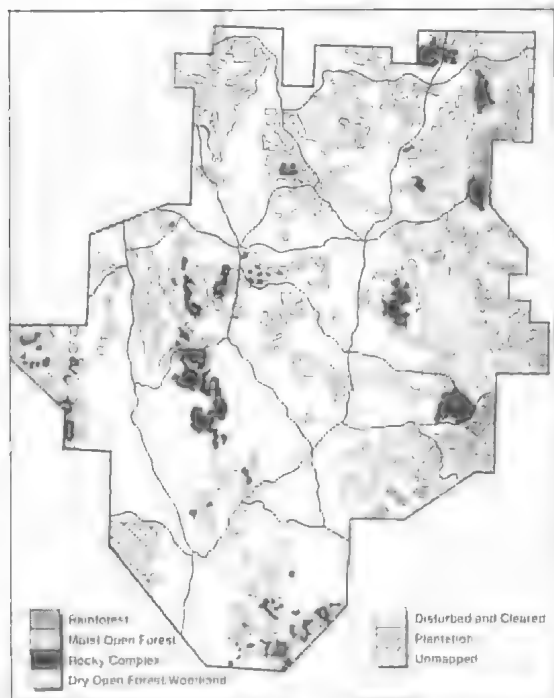


FIG. 5. Vegetational systems of the study area. Adapted from a computer-generated map incorporating recent data provided by the Armidale branch of the National Parks and Wildlife Service of New South Wales.

Moore suggests that more westerly records may yet be obtained from the New England area.

Eastern Dwarf Tree Frog *Litoria fallax* (Peters, 1880) (Fig. 12)

HABITAT: This species commonly lives among the floating and emergent vegetation at the margins of streams and large and small bodies of water. In coastal areas it is often found during the day sheltering in leaf-axils of pandanus, banana, pineapple plants, well away from water (Cogger, 1975).

RANGE: Coast, and adjacent mountains extending from southern Cape York Peninsula to southern N.S.W.

NEW ENGLAND RANGE: This frog is widely distributed across New England. The majority of records lie along the axis of the Great Dividing Range which suggests that elevation may be important in the distribution of this species. Noticeable hiatuses in distribution occur in the southwest and along the eastern escarpment. These are attributed to low collection effort in these areas. There is a surprising absence of records from the Walcha area which has been collected

several times. The western boundary of the study area coincides with the western limit for the species.

Dainty or Slender Green Tree Frog *Litoria gracilentia* (Peters, 1869) (Fig. 13)

HABITAT: This frog occupies a variety of habitats, reeds and floating vegetation in streams and swamps (Moore, 1961; Cogger, 1992), on roads and low vegetation (Barker & Grigg, 1977).

RANGE: The known range is extensive, along the eastern coastal areas of Australia from the top of Cape York to a little north of Sydney. It is extralimital in southwestern Papua (Cogger, 1992).

NEW ENGLAND RANGE: There are two records (1956, 1958) for Armidale. No further records in 33 years have occurred for this species and its status as part of the New England herpetofauna must be regarded as dubious. The Armidale locality suggests accidental or intentional transportation from the coast, perhaps in fruit or vegetables. The 1958 record is from Commissioners Waters, 5km east of Armidale. This creek receives the effluent from the Armidale sewerage works. There has also been significant land degradation adjacent to the creek over this period of time. Alternatively, the Tablelands may be too cold for this coastal species. These factors might account for the disappearance of this species from this locality, even if it had been accidentally established.

Broad-palmed Frog, Gunther's Frog *Litoria latopalmata* Günther, 1867 (Fig. 14)

HABITAT: Damp habitats everywhere, natural or artificial, so that it is found in the semi-arid interior as well as in the wetter coastal areas.

RANGE: Coast, ranges and interior of eastern Australia, central New South Wales to central Queensland (Cogger, 1992).

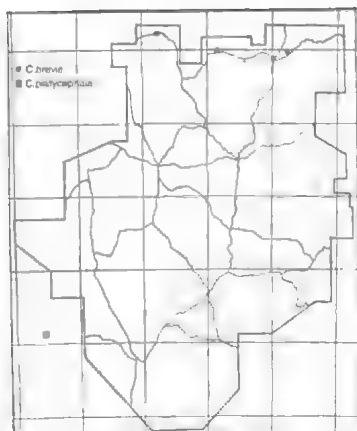
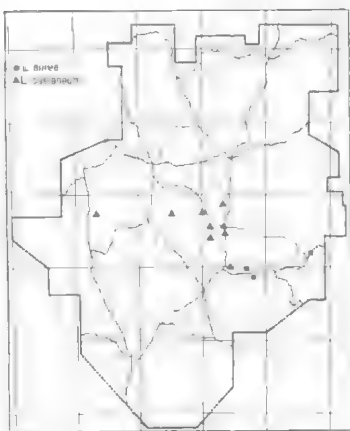
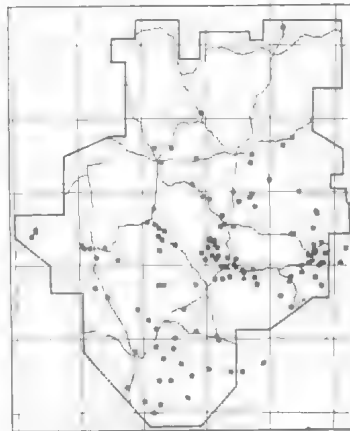
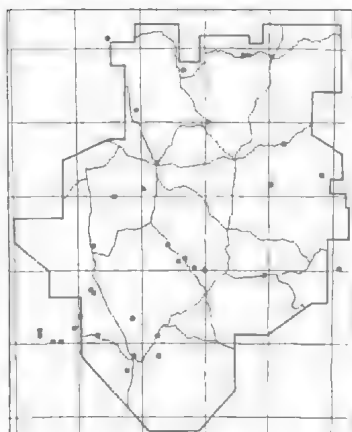
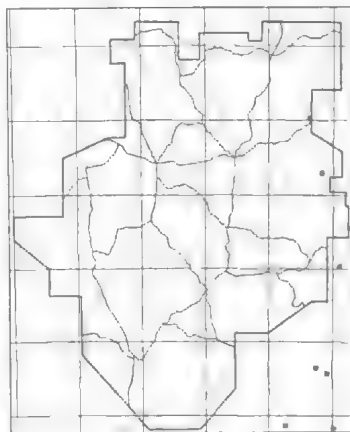
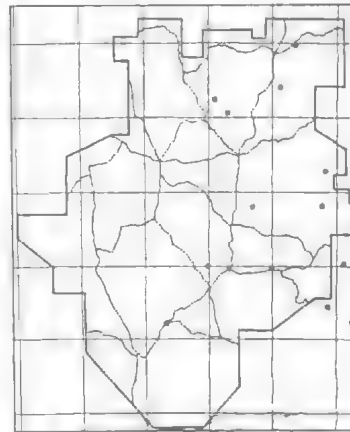
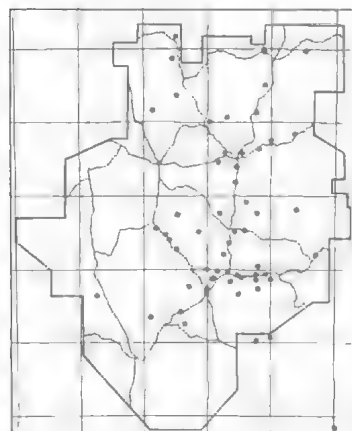
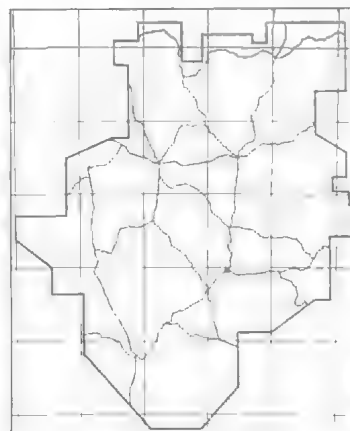
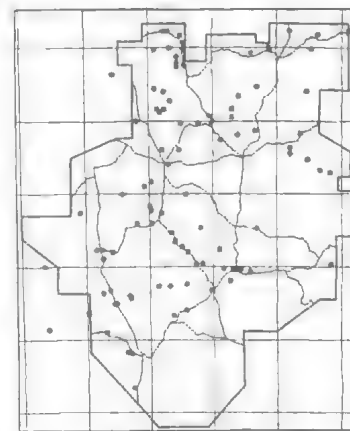
NEW ENGLAND RANGE: Widely distributed in the New England region. Very noticeable, however, is its apparent absence from large areas in the central and eastern parts of the study area which correspond approximately with the areas of rugged relief. The New England distribution is merely a small part of the total distribution of this widely ranging species.

Lesueur's Frog *Litoria lesueuri* (Duméril & Bibron, 1841) (Fig. 15)

HABITAT: Frequently associated with rocky or sandy rivers, it occupies, however, a wide variety of habitats; wet grass, coastal heathlands, dry sclerophyll and subtropical rainforest (Cogger, 1975).

RANGE: Coastal ranges and slopes of eastern Australia from northern Queensland to Victoria (Cogger, 1992).

NEW ENGLAND RANGE: Fig. 15 shows a wide distribution similar to that of the closely related *L. latopalmata*, including the central hiatus which may be

FIG. 6. *Cyclorana* spp.FIG. 7. *Litoria* spp.FIG. 8. *L. booroolongensis*FIG. 9. *L. caerulea*FIG. 10. *L. chloris*FIG. 11. *L. dentata*FIG. 12. *L. fallax*FIG. 13. *L. gracilentia*FIG. 14. *L. latopalmata*

due to collecting bias. Like that of *L. latopalmata*, the New England distribution is but a part of the wider distribution. It seems probable that the western boundary of New England marks the western limits of this species at these latitudes.

Rocket Frog *Litoria nasuta* (Gray, 1842) (Fig. 16)

HABITAT: Varied; swamps, coastal streams and lakes, tussock grassland, different kinds of shrubland, woodland and forest. Breeds in swamps.

RANGE: Coast and adjacent areas of northern and eastern Australia from the Kimberley region in north-west Australia to Cape York Peninsula thence to mid-coast N.S.W. Also in New Guinea.

NEW ENGLAND RANGE: One record comprising two specimens from the Moonbi Ranges south of Bendemeer in the southern part of the study area.

Peron's Tree Frog *Litoria peronii* (Tschudi, 1838) (Fig. 17)

HABITAT: Includes a wide variety of habitats in coastal and semi-arid areas, especially trees, and shrubs near streams, lagoons, swamps and dams.

RANGE: In southeastern Australia this species occupies the area east of a line joining Rockhampton in Queensland with Adelaide in South Australia and including northern Victoria.

NEW ENGLAND RANGE: Fig. 17 shows a distribution throughout New England with a concentration of records, i.e., collecting effort, around Armidale. In view of its wide distribution, this species must be presumed present, even in localities lacking records. It is apparent that the New England distribution of this species is just one small mosaic in the total geographic range.

Peppered Frog *Litoria piperata* Tyler & Davies, 1985 (Fig. 19)

HABITAT: This species, discovered in 1973 and described in 1985, occupies open forest, wet sclerophyll forest and sub-tropical rainforest.

RANGE: Endemic to New England where it is 'confined to the highlands ... at altitudes above 1000m' (Tyler & Davies, 1985). All records are from the eastern part of New England and lie within the higher rainfall zone (800-1100mm). *L. piperata* appears to be closely related to *L. phyllochroa* (Tyler & Davies, 1985). Concern is felt for the survival of this species.

Desert Tree Frog, Red Tree Frog *Litoria rubella* (Gray, 1842) (Fig. 20)

HABITAT: Moist tropical to arid regions; trees, shrubs, ground, adjacent to temporary or permanent water.

RANGE: Widely distributed across more than half of Australia except the southeastern sector. Found also in southern New Guinea.

NEW ENGLAND RANGE: This species is recorded only from the northwestern and southwestern part of New England, apparently the eastern limits for the species at this latitude. Table 1 shows that the majority (87%) of records occur below the 800mm isohyet. Most records occur in areas of low relief, with mid winter minimal temperatures ranging from $<0^{\circ}$ - 4° C.

Glandular Frog *Litoria subglandulosa* Tyler & Anstis, 1983 (Fig. 21)

HABITAT: Found in vegetation adjacent to rivers and creeks in cool, montane forest; also under bark on trees, among rocks and reeds, and beneath rotten logs, under stones, in sphagnum moss, and on roads at night. Elevation 1350-1450m (Tyler & Anstis, 1975).

RANGE: Records are from the New England tablelands and probably from near Girraween National Park, south of Stanthorpe (G. Ingram pers. comm., cited Tyler & Anstis, 1975). This species is also recorded south of the New England area from the Mt. Boss State Forest and from several sites in and around the Bulga State Forest in the Manning and Hastings Rivers district.

NEW ENGLAND RANGE: This species is distributed along the eastern edge of New England in areas of high elevation (800-1400m) and rainfall (1100-1499mm). Concentration of records in the Ebor-Pt. Lookout region reflects collecting bias. The New England distribution along the eastern boundary of the study area coincides with the edge of the escarpment. This species is closely related to the largely coastal *L. citropa* which extends from northeastern New South Wales to southeastern Victoria. The distribution of *L. subglandulosa* supports the opinion of Tyler & Anstis (1975) that this species probably replaces *L. citropa* on the Great Dividing Range of northern New South Wales.

Laughing Tree Frog (Ingram et al., 1993) *Litoria tyleri* Martin, Watson, Gartside, Littlejohn & Loftus-Hills, 1979 (Fig. 22)

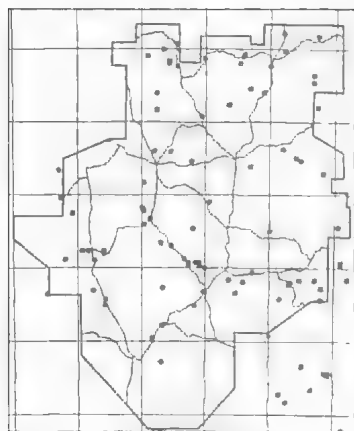
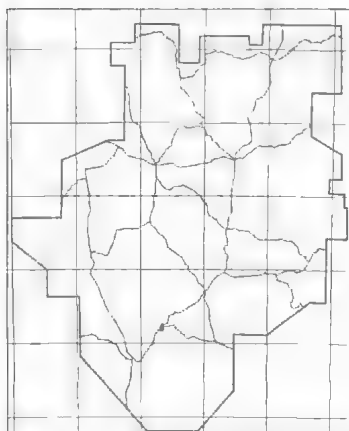
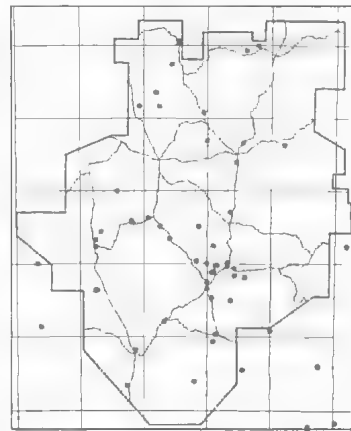
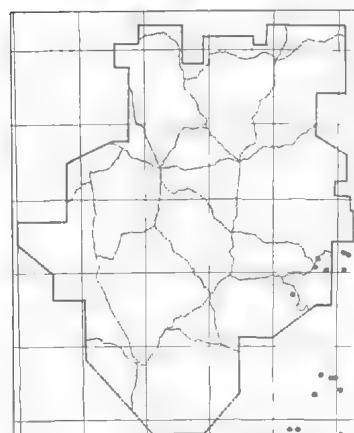
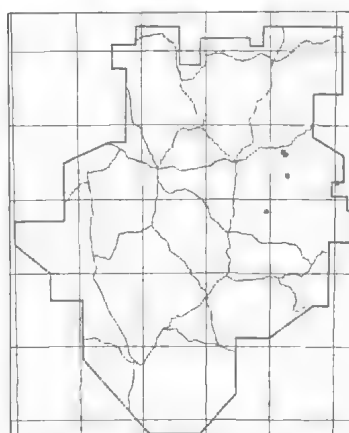
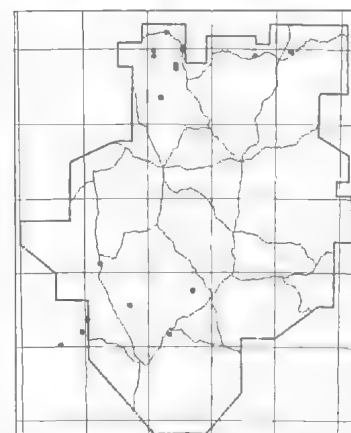
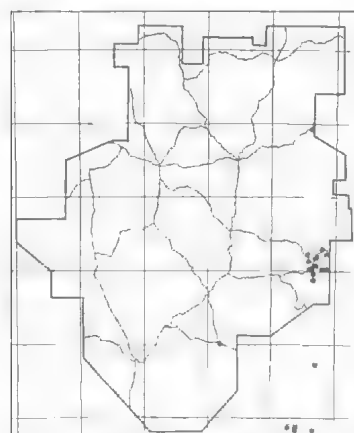
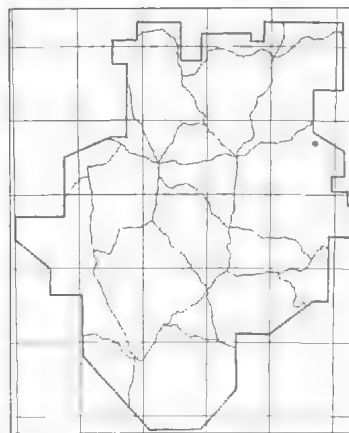
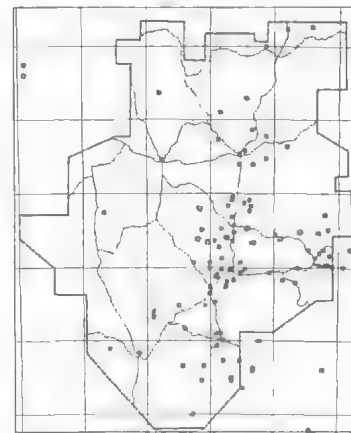
HABITAT: The New England specimen was calling from reeds in a small dam.

RANGE: Northeastern and southeastern coasts of Australia from southern Queensland to Jervis Bay, N.S.W.

NEW ENGLAND RANGE: The single record from the Barney Fire Trail in the Dalmorton State Forest lies within the coastal distribution of the total range for this species.

Verreaux's Tree Frog *Litoria verreauxii* (Duméril, 1853) (Fig. 23)

HABITAT: Associated with permanent water in a wide variety of habitats from coastal savannahs ascending through forest of different kinds to alpine grasslands.

FIG. 15. *L. lesueuri*FIG. 16. *L. nasuta*FIG. 17. *L. peronii*FIG. 18. *L. barringtonensis*FIG. 19. *L. piperata*FIG. 20. *L. rubella*FIG. 21. *L. subglandulosus*FIG. 22. *L. tyleri*FIG. 23. *L. verreauxii*

RANGE: Coast and ranges from central Victoria to central Queensland and the northern tablelands of New South Wales.

NEW ENGLAND RANGE: Fig. 23 shows the distribution to be almost ubiquitous east of about longitude 151°18' so that this species is barely represented in the western half of New England. Table 1 shows the distribution corresponds to elevations above 800m. (92%) and to rainfall above 700mm (97%) and with lower winter minimum temperatures.

FAMILY MYOBATRACHIDAE

Tusked Frog *Adelotus brevis* (Gunther, 1863) (Fig. 24)

HABITAT: Varied, generally riparian in wet forests or cleared country.

RANGE: Generally stated to be eastern Great Dividing Range and northern tablelands of New South Wales, and southern Queensland; Springwood west of Sydney (Moore, 1961).

NEW ENGLAND RANGE: The distribution west of the Great Dividing Range is greater than previously suspected, the species being well represented in all parts of the study area except the central and southwestern sectors, but even in this sector it has been recorded west of Tamworth. This species has wide ecological amplitude, occupying all minimum temperature zones below 4°C, all rainfall zones below 1500mm and all elevations below 1400m.

Pouched Frog, Hip-pocket Frog, Marsupial Frog *Assa darlingtoni* (Loveridge, 1933) (Fig. 25)

HABITAT: Thick leaf litter, under rocks and rotting logs in rainforest.

RANGE: MacPherson Ranges and adjacent mountains across the Queensland-New South Wales border.

NEW ENGLAND RANGE: Records are only from the Gibraltar Range National Park and the adjoining Washpool State Forest. The call also has been recorded from the Dorrigo National Park where this frog appears to be plentiful (J. Courtney, pers. comm.). These records probably represent the southern limit of this species and indicate a narrow adaptation to high rainforest along the edge of the escarpment.

Loveridge's Frog *Kyarranus loveridgei* (Parker, 1940) (Fig. 26)

HABITAT: Rain, Antarctic beech and cool temperate rainforest above 750m (Cogger, 1992). Lives 10-15cm below ground in soft, moist soil or mossy cavities beside streams (Moore, 1961; Cogger, 1992).

RANGE: Known only from the MacPherson Ranges on the Queensland/New South Wales border and from the Gibraltar Range National Park and Washpool State Forest of New South Wales.

NEW ENGLAND RANGE: The Gibraltar Range National Park and Washpool State Forest, which are on the eastern boundary of the study area. The ranges of *K. sphagnicolus* and *K. loveridgei* overlap in the Gibraltar Range National Park.

Sphagnum Frog *Kyarranus sphagnicolus* (Moore, 1958) (Fig. 27)

HABITAT: This frog was named from its discovery in 1951, deep inside a water-saturated clump of sphagnum moss in *Nothofagus* rainforest. However, at Pt. Lookout, the type locality, its habitat is not confined to sphagnum moss. It has been collected from water-filled burrows beneath rocks and logs. It also occupies crevices on wet cliffs and the water-permeated interstices of consolidated rock scree. Breeding burrows are associated with draining water, e.g., road gutters or scarcely perceptible seepages marking the head waters of gullies.

RANGE: There is a general north-south distribution along the Great Dividing Range in New South Wales from the Gibraltar Range National Park in the north to Elands in the south. The impression is of a number of separate populations strung along the high, wet points of the Great Dividing Range. To date there appear to be no records of this species from the Barrington Tops.

NEW ENGLAND RANGE: All records from this region are from the Gibraltar Range National Park, the Dorrigo National Park, New England National Park and the adjacent New England plateau. The altitudinal range extends lower than formerly thought; *K. sphagnicolus* occurs at Brinsville in the Bellingen Valley (H. Cogger, pers. comm.) at 106m, the site being cool and relatively sunless. (also see Discussion)

Fletcher's Frog *Lechriodus fletcheri* (Boulenger, 1890) (Fig. 28)

HABITAT: Rainforest and wet sclerophyll forest.

RANGE: Coastal and adjacent ranges from southeastern Queensland continuously to central New South Wales.

NEW ENGLAND RANGE: The eastern edge of the New England region represents the western extent of its habitat.

Eastern Banjo Frog, Pobblebonk, Four bolt Frog *Limnodynastes dumerilii* Peters, 1863 (Fig. 29)

HABITAT: Permanent waters, natural and artificial over a wide range of vegetational and climatic types. A burrowing species frequently dug from urban gardens.

RANGE: Widely distributed from southeastern South Australia, throughout Victoria, Tasmania and along the tablelands and coastal ranges into southeastern Queensland.

NEW ENGLAND RANGE: Broadly distributed throughout the study area. In New England its distribution overlaps that of *L. terraereginae*.

Long-thumbed Frog, Barking Frog, Marsh Frog *Limnodynastes fletcheri* Boulenger, 1988 (Fig. 30)

HABITAT: As for *L. tasmaniensis*. Typical localities are the edges of creeks and open water.

RANGE: Entirely west of the Great Dividing Range in southern Queensland and in the Murray Darling Basin of New South Wales, Victoria and South Australia.

NEW ENGLAND RANGE: Widespread on the New England tablelands and western slopes, but three records occur east of the Great Dividing Range.

Ornate Burrowing Frog *Limnodynastes ornatus* (Gray, 1842) (Fig. 31)

HABITAT: Wet coastal forests to arid inland.

RANGE: A broad sweep embracing the coastal and arid parts of southeastern New South Wales, Queensland, Northern Territory and northwestern Australia.

NEW ENGLAND RANGE: Widely dispersed through a range of habitats from rainforest to dry sclerophyll woodland. New England is a small part of the total range of this species.

Brown-striped Frog, Brown Frog, Striped Marsh Frog *Limnodynastes peronii* Duméril & Bibron, 1841 (Fig. 32)

HABITAT: Associated with slowly moving or static, permanent water, natural or artificial, in various vegetational types.

RANGE: Tasmania; coast and ranges of eastern Australia from Queensland to Victoria.

NEW ENGLAND RANGE: Predominantly the eastern side of the Great Dividing Range but extending to the western slopes of the tableland.

Salmon-striped Frog, Steindachner's Frog *Limnodynastes salmini* Steindachner, 1867 (Fig. 33)

HABITAT: Various types of woodlands. Swamps.

RANGE: Unusual, comprising coastal and adjacent areas of southern Queensland and northern New South Wales as well as central inland New South Wales.

NEW ENGLAND RANGE: Predominantly the south-western sector with some possibly anomalous records near Armidale. The New England records must represent the easternmost limits of this species in the area.

Spotted Grass Frog *Limnodynastes tasmanien-sis* Günther, 1858 (Fig. 34)

HABITAT: Near permanent waters, swamps, creeks and dams in a variety of habitats from semi-arid to moist coastal with a corresponding variety of vegetational types.

RANGE: Tasmania, eastern South Australia, all of Victoria and New South Wales, southern and eastern Queensland as far north as Cooktown.

NEW ENGLAND RANGE: Ubiquitous, yet representing only a minute part of the total range of this widely distributed species

Northern Banjo Frog, Northern Bull Frog *Limnodynastes terraereginae* Fry, 1915 (Fig. 35)

HABITAT: Similar to that of *L. dumerilii*.

RANGE: Occurs coastally from Cape York, Queensland to northern New South Wales, thence along the western slopes of the Great Dividing Range, extending to eastern central New South Wales. Westward extent unknown.

NEW ENGLAND RANGE: The few records of this species for the study area are widely spaced and obviously part of the southern distribution of this species which extends to Tomingley in New South Wales (Martin, 1972).

Stuttering Frog *Mixophyes balbus* Straughan, 1968 (Fig. 36)

HABITAT: Wet sclerophyll and subtropical rainforest. **RANGE:** Eastern side of the Great Dividing Range in southern Queensland, N.S.W. and Victoria.

NEW ENGLAND RANGE: A part of the wider distribution extending north to south along the eastern side of the Great Dividing Range.

Great Barred Frog *Mixophyes fasciolatus* Günther, 1864 (Fig. 37)

HABITAT: Coastal and adjacent ranges.

RANGE: Southeastern Queensland to southern N.S.W.

NEW ENGLAND RANGE: Like *M. balbus*, it has been found only along the eastern edge of the northern tablelands.

Great Barred Frog, Southern Barred Frog, Giant Barred Frog *Mixophyes iteratus* Straughan, 1968 (Fig. 37)

HABITAT: Wet sclerophyll forests and riverine rainforests of coastal eastern Australia.

RANGE: Exclusively coastal from Bunya Bunya mountains in southeastern Queensland almost to the New South Wales-Victorian border.

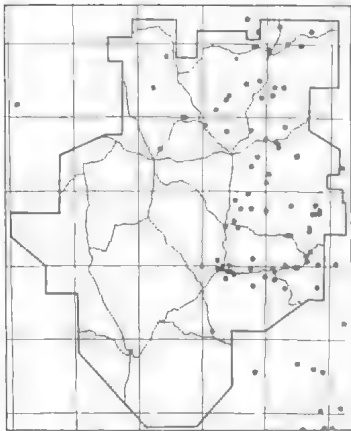


FIG. 24. *Adelotus brevis*

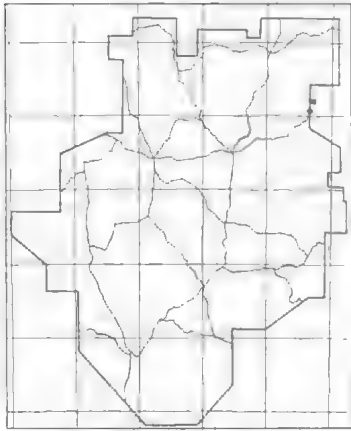


FIG. 25. *Assa darlingtoni*

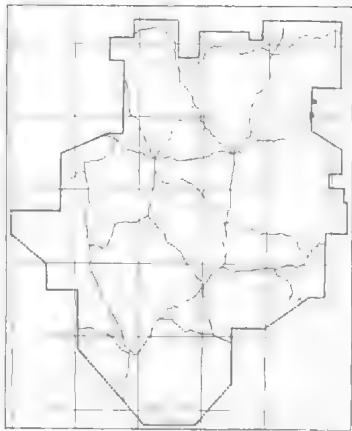


FIG. 26. *Kyrranus loveridgei*

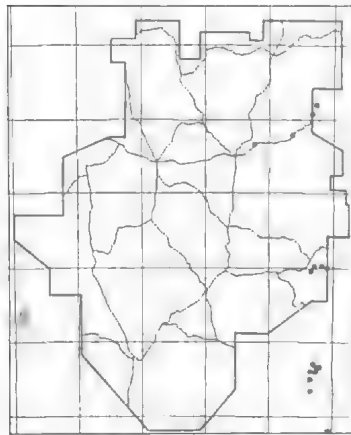


FIG. 27. *K. sphagnicolus*

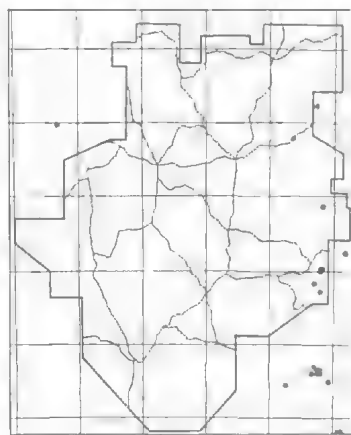


FIG. 28. *Limnodynastes fletcheri*

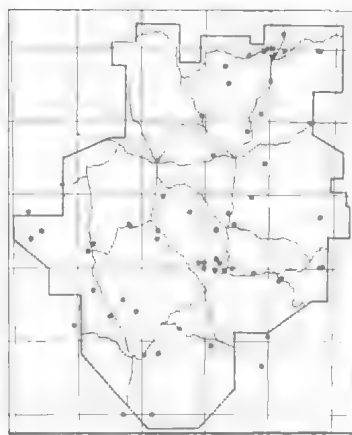


FIG. 29. *Lim. dumerila*

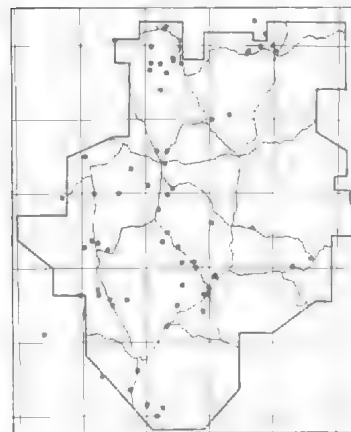


FIG. 30. *Lim. fletcheri*

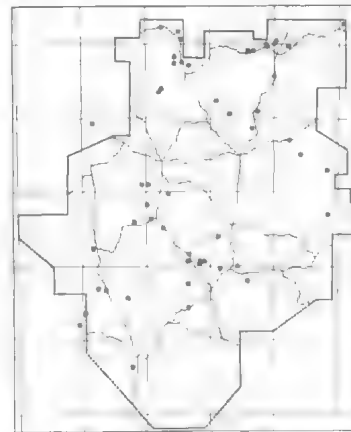


FIG. 31. *Lim. ornatus*

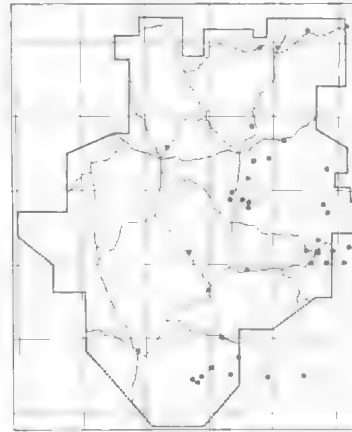


FIG. 32. *Lim. personatus*

NEW ENGLAND RANGE: The few records are from the eastern boundary of the study area, from the Gibraltar Range in the north and from the coastal forests east of Pt. Lookout.

Spotted Burrowing Frog, Painted Frog, Spadefoot Toad *Neobatrachus sudelli* (Lamb, 1911) (Fig. 38)

HABITAT: A burrowing species in habitats ranging from inland deserts to the forests of the western slopes of the Great Dividing Range.

RANGE: Southeastern South Australia, northern Victoria, inland to the Great Dividing Range in New South Wales and southern Queensland.

NEW ENGLAND RANGE: The few records span the New England region and unexpectedly includes one from Pt. Lookout east of the Great Dividing Range.

Holy Cross Toad, Crucifix Toad *Notaden bennettii* Günther, 1873 (Fig. 39)

HABITAT: The dry areas of inland New South Wales and southern Queensland, especially the black-soil flood plains of the larger rivers. Found in a variety of vegetational types.

RANGE: The plains of New South Wales and southern Queensland west of the Great Dividing Range.

NEW ENGLAND RANGE: There are only three records for the New England region. That from Armidale on the tablelands is unexpected and may represent a transported individual.

Red-Crowned Toadlet *Pseudophryne australis* (Gray, 1835) (Fig. 42)

RANGE: Long believed to be restricted to the Hawkesbury Sandstone about Sydney.

NEW ENGLAND RANGE: The three positively identified, widely separated records from New England appear anomalous in relation to the well known association of this species with the Hawkesbury Sandstone. The identity of the specimens is confirmed (K. Thumm, pers. comm.) but there is some question as to their provenance. The problem is to be discussed in a forthcoming work by Karen Thumm of the University of Newcastle.

Brown Toadlet, Bihron's Toadlet *Pseudophryne bibronii* Günther, 1858 (Fig. 40)

HABITAT: Virtually every habitat within its range. Wetter coastal areas to drier inland habitats, lowlands to mountains; shelters under logs, rocks, surface debris; associated with temporary or static permanent waters, puddles and ponds.

RANGE: Distributed widely from southeastern South Australia through Victoria, Tasmania, coastal and inland New South Wales and southeastern Queensland.

NEW ENGLAND RANGE: Virtually ubiquitous in the New England region which is a small part of the total range. The westernmost records may represent the western limits for the species in this region.

Keferstein's Toadlet, Red-backed Toadlet *Pseudophryne coriacea* Keferstein 1858 (Fig. 41)

HABITAT: Generally in forest litter, under stones, in grass near streams and marshy areas. In the New England region it is associated with wet sclerophyll forest, and temperate rainforest, where it occurs under logs, rocks and in dense, moist vegetation and leaf litter.

RANGE: Coastal and adjacent ranges from southeastern Queensland to northern New South Wales.

NEW ENGLAND RANGE: A conspicuously eastern distribution coinciding closely with the Great Dividing Range, which marks the western limit of this species.

Large Toadlet *Pseudophryne major* Parker, 1940 (Fig. 42)

HABITAT: Except that it is found in situations similar to those of *P. bibronii* in other parts of Australia, little is known concerning this species.

RANGE: There is some difference of opinion as to its range. Cogger (1992) records its distribution as from Cape York to southeastern Queensland. Barker & Grigg (1977) restrict this species to the Burnett River valley in southeastern Queensland. Ingram & Corben (1994) remarked that occurrences of *P. major* in southern and central Queensland were valid, and reported several isolated populations in far north Queensland.

NEW ENGLAND RANGE: Records for this species in the New England region are three specimens QMJ534231-3 from the Queensland Museum, collected at Mt Kaputar near the central western boundary of the study area. Identification has been confirmed and the presence of this species in such a westerly part of New England represents a remarkable extension of range.

Eastern Sign-bearing Froglet *Ranidella parinsignifera* Main, 1957 (Fig. 43)

HABITAT: '*R. parinsignifera* occupies the drier areas inland to the west of the Great Dividing Range and generally inhabits the summer-dry ponds of the region.' (Littlejohn, 1958).

RANGE: Murray River Valley in South Australia and Victoria, through central-western New South Wales and southern Queensland where it reaches the coast.

NEW ENGLAND RANGE: Within the region a wide distribution west of the Great Dividing Range, with a number of records occurring east of the Range and even of the study area. The range overlaps that of *R. signifera* q.v. and is contained comfortably within the total range.

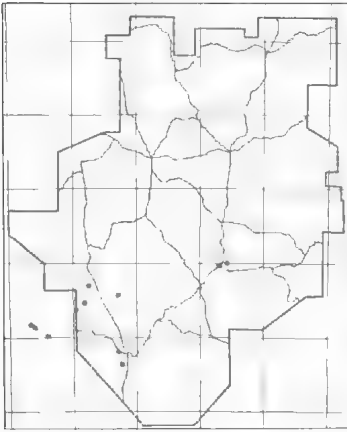


FIG. 33. *Lim. salmii*

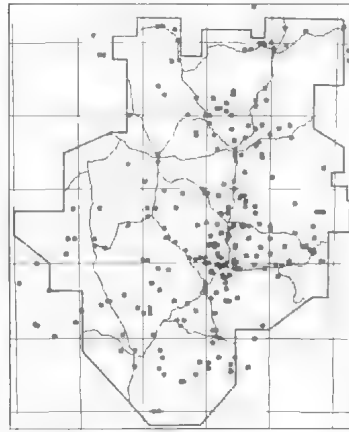


FIG. 34. *Lim. tasmaniensis*

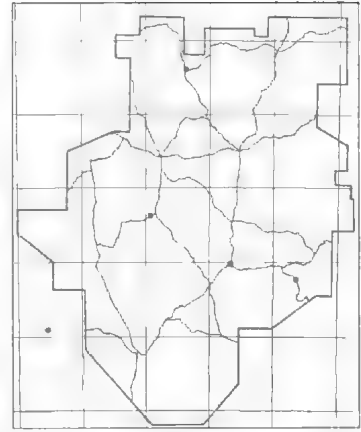


FIG. 35. *Lim. terraereginae*

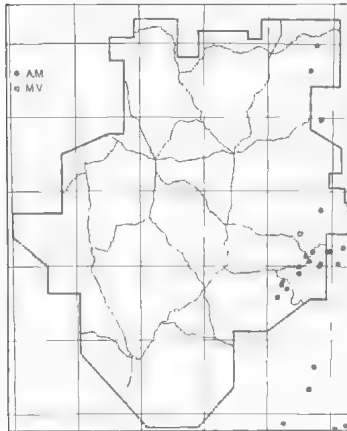


FIG. 36. *Mixophyes balbus*

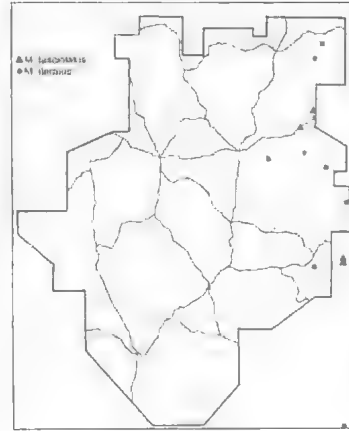


FIG. 37. *Mixophyes sp.*

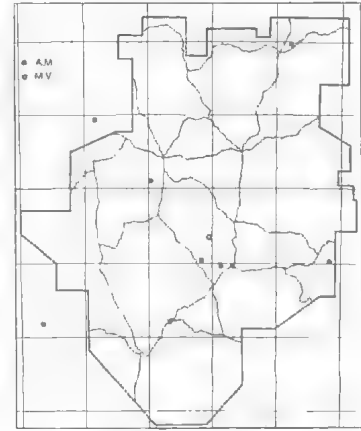


FIG. 38. *Neobatrachus sudelli*

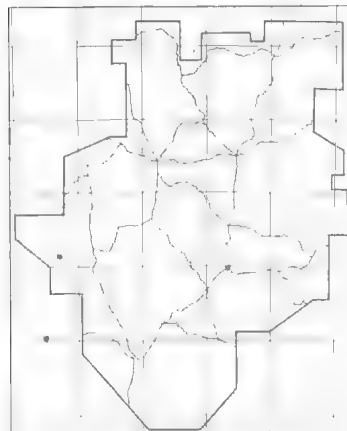


FIG. 39. *Notaden bennettii*

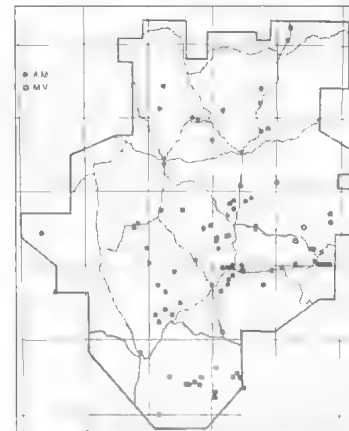


FIG. 40. *Pseudophryne bibronii*

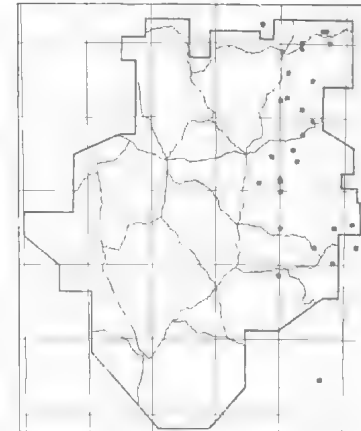


FIG. 41. *P. verticea*

Common Eastern Froglet *Ranidella signifera* Girard, 1853 (Fig. 44)

HABITAT: Moist or wet situations in any part of its range.

RANGE: Widely distributed along the coastal and western sides of the Great Dividing Range from southeastern Queensland to South Australia. Also in Tasmania.

NEW ENGLAND RANGE: Almost ubiquitous.

Yellow-spotted Toadlet, Smooth Toadlet *Uperoleia laevis* Keferstein, 1867 (Fig. 45)

HABITAT: Moist situations in a variety of habitats, e.g. under logs, stones and edges of lagoons.

RANGE: Central and southeastern coastal regions of southeastern Australia. Also on the Great Dividing Range as far north as Blackdown Tableland, Queensland (Davies & Littlejohn, 1986).

NEW ENGLAND RANGE: Almost ubiquitous, unrecorded only from the extreme western and southern parts of the study area.

Andersson's Toadlet, Wrinkled Toadlet *Uperoleia rugosa* (Andersson, 1916) (Fig. 46)

HABITAT: As for *U. laevis*.

RANGE: South-central Queensland and New South Wales to the Victorian border, extending to the coast in Queensland and northern New South Wales.

NEW ENGLAND RANGE: All records derive from the northwestern quadrant.

Tyler's Toadlet *Uperoleia tyleri* Davies & Littlejohn, 1986 (Fig. 46)

HABITAT: Presumably similar to that of *U. laevis*.

RANGE: Coastal southeastern Australia, Victoria and New South Wales. Also Tamworth, New South Wales.

NEW ENGLAND RANGE: Known only from one old (4.iv. 1910) record from Tamworth, New South Wales which is unusual in being widely separated from the nearest coastal records.

RESULTS AND DISCUSSION

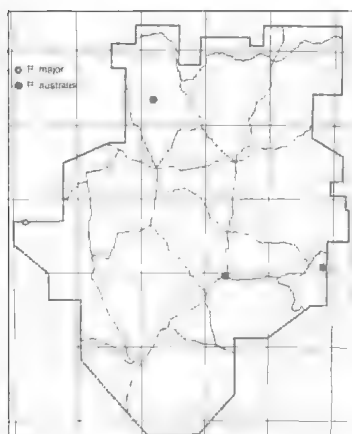
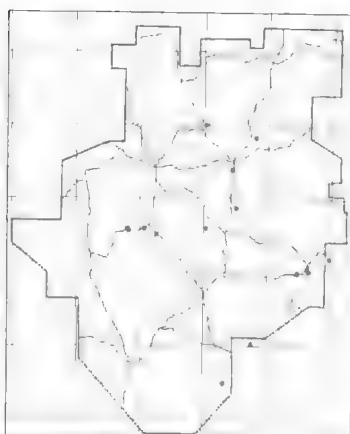
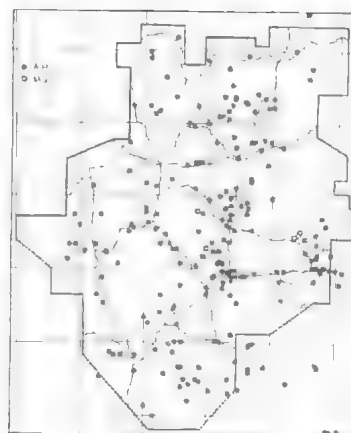
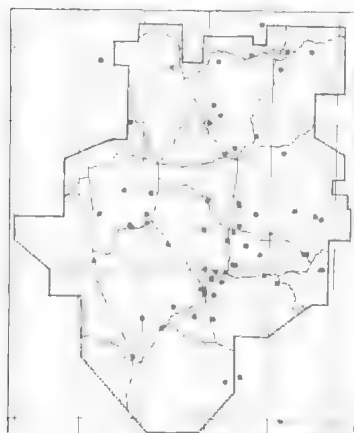
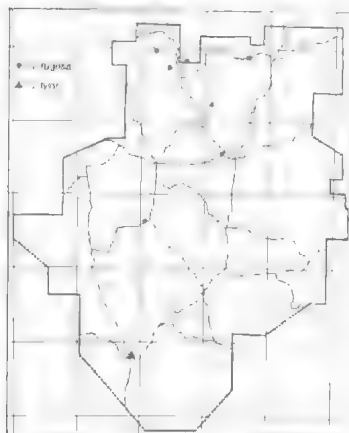
There are about 195 native species of frogs in 27 genera and 4 families reported so far from Australia (Cogger, 1992). Thus, the New England frog fauna (46 species) constitutes 24% of the known Australian species, and the area has 48% of the Australian genera and 50% of the Australian families represented. The area of New England is 0.49% of the total area of Australia and therefore it is well endowed with frog species compared with the country as a whole. This probably can be attributed to the moderately abundant rainfall of the region, in a generally dry continent,

an important consideration for such a generally moisture-sensitive group as amphibians. Lower temperatures on the tablelands than in much of Australia may bar some species from the area. The main reason, however, is that the New England region has a wide range of elevation and rainfall and that it overlaps three regions of the Kosciuskan zoogeographic region. (Ford & Macfarland, 1991). Thus, it forms an interchange zone between northern and southern and between eastern and western species. Compilation of data from Cogger (1992) shows that adjoining coastal areas of the same latitudinal span but with milder temperatures because of lower elevation have about 35 species, and northern tropical and subtropical areas have a still richer frog fauna, (approximately 119 species). Thus, New England is low in species richness compared to tropical Australia, slightly richer than adjoining temperate, but milder, moister coastal areas, and far richer than arid central Australia (25 species). Arid areas of an equivalent size to New England would have even fewer species.

The native Australian families not present in the New England region are the Microhylidae and the Ranidae. The former is a family represented in Australia by 17 species in two genera (*Cophixalus* and *Sphenophryne*), all are restricted to the tropical north. The Ranidae are represented in Australia by only one species, *Rana daemeli*, found only on Cape York Peninsula and Western Arnhem Land.

The introduced cane toad, *Bufo marinus*, the sole species of the family Bufonidae in Australia, has not spread to the New England region despite having reached northeastern New South Wales. It is unlikely to become established in New England because it probably could not survive the low winter temperatures there (van Beurden 1981).

The distribution of each species (Figs. 6-44) was compared with the geographic patterns of four environmental factors, the midwinter minimum temperature, the mean annual rainfall, elevation and vegetational zonation and the results were collected in Table 1 which shows this analysis in relation to the seven patterns of anuran distribution ascertained for the New England area (see below). It should be pointed out that in New England the environmental factors employed follow approximately the east-west topographical gradient which generally is highest in the east and lowest in the west. Figs 2-5 show that in general the lower range of these environmental values occurs in the western parts of New England and

FIG. 42. *Pseudophryne* spp.FIG. 43. *Ramidella parinsignifera*FIG. 44. *R. signifera*FIG. 45. *Uperoleia laevigata*FIG. 46. *Uperoleia* spp.

the higher ones in the east along and eastward from the Great Dividing Range. It is evident that many species have wide ranges across one or more environmental parameters. Within this wider range 30% or more of site records for each species occur across narrower ranges of environmental values.

Table 2 shows the vegetational context of frog distribution in the New England region.

Table 1 shows that with the exception of the eastern group, 30% of all site records occupy the lower half of the scale in relation to winter minimum temperature, mean annual rainfall, and vegetational zonation. In the eastern species there is a marked tendency to the upper half of the scale in respect of rainfall and vegetation. The single central species *Litoria castanea* is, however, mid-range for altitude and rainfall.

The middle ranges of elevation are occupied by 27/46 (59%) of species with the exception of northern and western species which despite some variability do tend to lower altitudes.

Very striking is the distribution of New England frogs in relation to vegetational zonation in that more than 30% of site records for each of 35/46 (80%) of species are found in the DR+CL zone (Table 1).

Concentration of site records in this zone is actually much greater than is suggested by these numbers. A high mean of 78.75 (61-88)% of total site records for these 35 species falls in this particular vegetational zone (Table 2). Perhaps this should not be surprising since Table 2 shows this zone to comprise 70% of New England. This zonal concentration implies considerable collecting bias, most of the main road system being located in this zone. Despite this the authors

believe the records provide a good indication of the environmental distribution for species with a high number of site records. Some doubt must be expressed in relation to the many species for which site records are few but even these tend to fall into eastern or western profiles.

The distributional patterns of the New England frogs fall into seven groups:

Eurytopic species (Table 1; U). These are widely distributed in the area, being represented at sites scattered throughout the entire region. The species in this category are *Limnodynastes dumerilii*, *L. ornatus*, *L. tasmaniensis*, *Pseudophryne bibronii*, *Ranidella signifera*, *Up-e-roleia laevigata*, *Litoria booroolongensis*, *L. caerulea*, *L. fallax*, *L. latopalmata*, *L. lesueuri* and *L. peronii*. Of these, only *L. booroolongensis* has a restricted distribution outside the area. It occurs only in east central New South Wales, but the borders of its range extend well beyond the limits of the New England area. *L. caerulea* is widely distributed from arid east-central Australia to the coast and throughout the tropical north; its range extends well beyond the boundaries of New England in all directions. It is recorded from nearly all parts of New England, but sparsely. *L. fallax* and *L. lesueuri* occupy a narrow strip along most of the eastern Australian coast. Their ranges do not extend very far westward of the New England boundaries and it may be significant that the former was seldom collected in the southwestern part of the area. *L. latopalmata* occupies a large, roughly triangular distribution, the base extending along the coast from northeastern Queensland to southeastern New South Wales and the apex reaching the junction of the New South Wales and South Australian borders. *U. laevigata* is found throughout coastal eastern New South Wales and Victoria. *R. signifera*, *L. dumerilii*, and *P. bibronii* are widely distributed in southeastern Australia. *L. tasmaniensis* covers nearly the eastern third of the continent and *L. peronii* has a southeastern range not much smaller. *L. ornatus* extends from just south of New England northward and across the top of Australia. Cogger (1992) reported almost all of these species as being found in a variety of habitats or in places away from water. The exceptions were *L. dumerilii* which occupies permanent water of various sorts and *L. booroolongensis* which is mainly found in mountain streams. Thus, with the exception of *L. booroolongensis*, these are widely distributed species with wide ecological amplitude and/or terrestrial tendencies. These 12 species make up

26% of the frog species of the New England region.

The wide range of environmental zones shown by the 12 nearly ubiquitous species reflects their wide distribution. Although this group is adapted to a wide range of conditions there is at the 30% site record level a marked tendency towards the lower end of the respective environmental ranges.

Eastern species (Table 1, E, E+, E++). These are found only in the eastern part of the New England region. They constitute the second largest group in the area (14 species; 30%). Ten of them (E) are restricted to the extreme edge of the region and scarcely get inside the New England borders. These are *Assa darlingtoni*, *Kyarranus loveridgei*, *K. sphagnicolus*, *Lechriodus fleischeri*, *Mixophyes balbus*, *M. fasciolatus*, *M. iteratus*, *Litoria chloris*, *L. barringtonensis* and *L. subglandulosa*. They have narrow, strip-like eastern distributions in eastern Australia and their marginal entry into the New England region represents the western edges of their ranges. All are inhabitants of wet forests, (*L. chloris* is largely arboreal, the others terrestrial), such as Antarctic beech forest, rainforest and wet sclerophyll forest and their range in New England reflects the limited amount of such habitat in the region.

Except for vegetational cover, the purely eastern species have a much narrower range for all environmental parameters than do the eurytopic species. This is true even of species with more than just a few site records. Temperature and elevational ranges are narrow, predominantly middle range, while the quite narrow, rainfall ranges are to the high side of the scale, corresponding to the higher elevations of the wet forests occupied by these species. It is interesting that even at the 20% level of site records, eastern species occupy a greater variety of vegetational types compared with eurytopic species (Table 1). Indeed, two eastern species *L. barringtonensis* and *L. subglandulosa*, are found even in the DR + CL zone which for these species lies mainly in the high rainfall areas. Three eastern species have a wider range of elevation and rainfall than do other members of this group.

K. sphagnicolus, inside the boundaries of New England, is distributed along the Great Dividing Range at elevation between 800m and > 1400m but 88% of site records lie more narrowly between 800 and 1200m. It is worth noting that this species also occupies the adjoining wet forests of the steep coastal slopes of the escarpment down to altitudes of 106m (Brinerville; H. Cogger, pers. comm.), 300m (Beechwood; AMR118198-207),

327m (Forbes River, Cowarral; AMR104114), 370m and 620m (Mistake State Forest near Bowraville; (J. Monro, pers. comm.).

M. balbus ranges from 0 to >1400m but like others of its group, 30% of its site records lie more narrowly in rainfall zone 3. Some 77% of its site records fall between 800 and 1300m. A further 6% are found at >1400m. The 18% of elevation records below 799m represent high rainfall coastal sites penetrating the Tableland via the gorges.

The geographical range of *M. fasciolatus* is greater than those of other eastern species (Figs 36, 37), extending as it does to the vicinity of Red Range near Glen Innes. Even so, this most westerly record still lies east of the Great Dividing Range (Figs 1, 37).

The small number of site records for each species of *Mixophyes* imposes caution but there is some indication that *M. fasciolatus* (58% of records) occurs at lower altitudes than does *M. balbus* (18%). More than half of the few records of *M. fasciolatus* are situated in lower coastal altitudes whereas more than half the records of *M. balbus* lie in the higher altitude zones. These two species, with *L. subglandulosa*, occur over a wider range of elevation, rainfall and vegetational types than do other eastern species (Table 1).

Four species (Table 1; E++), *Adelotus brevis*, *Limnodynastes peronii*, *Litoria dentata* and *L. verreauxii*, have wider distributions that encompass approximately the eastern half of the New England area. All occupy relatively wet habitats and all have extensive geographic ranges that include the eastern coast and the Great Dividing Range, the western limits lying within New England. The environmental correlations of these four species are very similar to that of the eurytopic species corresponding to the extensive distributional overlap of the two categories.

Pseudophryne coriacea (Table 1, E+) is intermediate between the other two eastern groups. It occupies a strip along the eastern edge of New England but is not so restricted as the first-mentioned group. Whereas west of the Great Dividing Range there are no E records and at least one third of E++ records only 2/27 of *P. coriacea* records occur here. This slightly more extensive geographic range coincides with a slightly wider temperature range of July minimum temperature and generally with a cooler, drier environment than is true for purely eastern species.

P. coriacea shares with the aforementioned species of *Mixophyes* a similar range of elevation

and rainfall but in respect to vegetation all site records of this species are from DR + CL and DF + WDL zones. (Table 1,2).

Western species (Table 1; W). Three species have distributions opposite to those of the above group, occupying predominantly the western part of New England. They are *Limnodynastes fletcheri*, *L. salmini* and *Litoria rubella*. Of these the first two have extensive distributions in the drier western plains of New South Wales and adjacent areas extending northward into Queensland to or near the coast. *L. salmini* is cryptic or burrowing and found only after rains. *L. fletcheri*, is not so arid-adapted but is secretive except after rains. Occupying about the western two thirds of the region, it has a broader distribution in New England than do the other two. *L. rubella*, appropriately called the Desert Tree Frog, occurs throughout the central deserts of Australia and the entire tropical north. It covers over two thirds of Australia, yet its southeastern boundary runs through New England where it is found only in the north and southwest. A fourth species, *Ranidella parinsignifera*, is also a burrowing, cryptic species with an extensive distribution in the drier areas of western New South Wales. Contrary to expectations, in New England it has a central to eastern distribution being virtually unrepresented in western New England. It is included here on the basis of its general distribution. Another burrowing species, *Cyclorana platycephala*, occurs just outside the study area.

Excluding *C. platycephala*, all western species have a wide elevational range and their distributions tend towards the lower end of the minimum temperature and rainfall scales. *R. parinsignifera*, however, is unique among all groups of species in extending over four zones of rainfall at the 20% of site records level. With the eastern group it is remarkable, too, for the concentration of 30% of its site records at higher elevations (85%), an aspect shared with *P. bibroni* (85%), *L. subglandulosa* (82%) and *L. castanea* (77%).

Northern Species (Table 1; N). Two species are found only in the northern part of New England. They are *Cyclorana brevipes* and *Uperoleia rugosa*. *U. rugosa* is a species from a wide variety of habitats and an overall distribution from southern Queensland south in a wide band to Victoria. In New South Wales its distribution is mainly west of the New England region despite it being coastal in northern New South Wales and Queensland. Although it extends south of New England, it does so farther inland, just catching the northwestern tip of the region in its range. The

TABLE 1. Environmental profiles of the New England frogs (% site records - all values rounded off). See Appendix for environmental codes.

| Gp. | Species | July Min. C | | | | | Elevation (m) | | | | | Rainfall (mm) | | | | | | | Vegetation | | | | |
|----------|-----------------------------|-------------|-----|----|-----|----|---------------|----|-----|----|----|---------------|-----|----|----|-----|----|----|------------|----|-----|----|-----|
| | | N | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 |
| U | <i>Lit. booroolongensis</i> | 123 | 33 | 29 | 37 | | 2 | 33 | 44 | 21 | | 8 | 36 | 23 | 15 | 12 | 7 | | 77 | 2 | 17 | 1 | 2 |
| U | <i>Lit. caerulea</i> | 28 | 29 | 43 | 25 | | 11 | 54 | 36 | | | 21 | 46 | 21 | 11 | | | | 86 | 4 | 11 | | |
| U | <i>Lit. fallax</i> | 58 | 52 | 41 | 7 | | 2 | 16 | 66 | 16 | | 9 | 41 | 29 | 19 | 2 | | | 79 | 2 | 17 | 2 | |
| U | <i>Lit. latopalmata</i> | 95 | 38 | 35 | 26 | | 17 | 51 | 32 | 1 | | 36 | 40 | 16 | 7 | 1 | | | 81 | 5 | 12 | 2 | |
| U | <i>Lit. lesueuri</i> | 76 | 37 | 37 | 26 | | 15 | 46 | 40 | | | 24 | 42 | 12 | 9 | 8 | 5 | | 61 | 1 | 13 | 1 | |
| U | <i>Lit. peronii</i> | 48 | 41 | 47 | 10 | 2 | 8 | 31 | 56 | 4 | | 19 | 48 | 27 | 6 | | | | 88 | 2 | 8 | 2 | |
| U | <i>Lim. dumerilii</i> | 60 | 25 | 48 | 27 | | 5 | 25 | 52 | 18 | | 8 | 43 | 32 | 12 | 2 | 3 | | 75 | 5 | 10 | 8 | 2 |
| U | <i>Lim. ornatus</i> | 50 | 25 | 56 | 18 | | 16 | 44 | 38 | 2 | | 28 | 42 | 22 | 6 | | 2 | | 82 | 2 | 16 | | |
| U | <i>Lim. tasmaniensis</i> | 259 | 39 | 37 | 23 | 2 | 5 | 17 | 58 | 20 | | 9 | 34 | 33 | 20 | 4 | 1 | | 88 | 2 | 8 | | 1 |
| U | <i>P. bibronii</i> | 94 | 36 | 31 | 27 | 6 | 1 | 14 | 53 | 32 | | 4 | 16 | 36 | 33 | 5 | 5 | | 70 | 5 | 15 | 3 | 2 |
| U | <i>R. signifera</i> | 208 | 35 | 34 | 29 | 3 | 3 | 31 | 47 | 18 | 2 | 11 | 41 | 18 | 21 | 5 | 4 | 1 | 82 | 2 | 11 | 2 | 2 |
| U | <i>U. laevigata</i> | 63 | 32 | 51 | 16 | 2 | 2 | 20 | 64 | 14 | | 5 | 49 | 18 | 21 | 5 | 3 | | 76 | 6 | 14 | | 3 |
| E | <i>Lit. chloris</i> | 2 | | | 100 | | | 50 | 50 | | | | | | | 50 | 50 | | | | 50 | | 50 |
| E | <i>Lit. barringtonensis</i> | 4 | | | 100 | | | 50 | 50 | | | | | | | 75 | 25 | | 50 | | | 25 | 25 |
| E | <i>Lit. subglandulosa</i> | 17 | | | 100 | | | | 18 | 82 | | | 6 | | 6 | 53 | 41 | | 35 | 24 | 6 | 18 | 18 |
| E | <i>Assa darlingtoni</i> | 2 | | | 100 | | | 50 | 50 | | | | | | | 100 | | | | | | | 100 |
| E | <i>K. loveridgei</i> | 2 | | | 100 | | | 50 | 5 | 0 | | | | | | 100 | | | | | | | 100 |
| E | <i>K. sphagnicolus</i> | 8 | | 13 | 88 | | | 25 | 63 | | 12 | | | | 13 | 38 | 38 | 13 | 25 | | | 25 | 50 |
| E | <i>Lech. fletcheri</i> | 8 | | | 100 | | 12 | 38 | 50 | | | | | | 13 | 50 | 38 | | | | 37 | 13 | 50 |
| E | <i>M. balbus</i> | 17 | | | 100 | | 6 | 12 | 53 | 24 | 6 | | | | 29 | 41 | 29 | | 7 | 13 | 33 | 33 | 13 |
| E | <i>M. fasciolatus</i> | 7 | | 14 | 86 | | 29 | 29 | 29 | 29 | | | | 14 | 43 | 29 | 14 | | 29 | | 43 | 29 | |
| E | <i>M. iteratus</i> | 2 | | | 100 | | | | 100 | | | | | | | 100 | | | | | | 50 | 50 |
| E+ | <i>P. coriacea</i> | 27 | 7 | 61 | 32 | | 4 | 15 | 67 | 15 | | | 4 | 7 | 59 | 19 | 11 | | 44 | 7 | 33 | 11 | 4 |
| E++ | <i>Lit. dentata</i> | 11 | 36 | 46 | 18 | | 9 | 9 | 73 | 9 | | | 27 | 27 | 36 | 7 | | | 82 | | 18 | | |
| E++ | <i>Lit. verreauxii</i> | 100 | 39 | 28 | 29 | 4 | | 8 | 63 | 29 | | 3 | 32 | 29 | 22 | 8 | 6 | | 82 | 1 | 13 | 1 | 3 |
| E++ | <i>Adel. brevis</i> | 89 | 33 | 45 | 20 | 1 | 5 | 15 | 65 | 16 | | 3 | 28 | 19 | 34 | 11 | 5 | | 72 | 1 | 25 | 1 | 1 |
| E++ | <i>Lim. peronii</i> | 37 | 22 | 24 | 46 | | 3 | 11 | 49 | 27 | 11 | 3 | 19 | 22 | 30 | 19 | 8 | | 65 | 5 | 22 | 3 | 5 |
| N | <i>C. brevipes</i> | 2 | | 50 | 50 | | | 50 | 50 | | | 100 | | | | | | | 100 | | | | |
| N | <i>U. rugosus</i> | 7 | 43 | 57 | | | 29 | 57 | 14 | | | 43 | 43 | 14 | | | | | 86 | | 14 | | |
| W | <i>C. platycephala</i> | 1 | | | 100 | | 100 | | | | | 100 | | | | | | | 100 | | | | |
| W | <i>Lit. rubella</i> | 15 | 13 | 53 | 33 | | 40 | 40 | 20 | | | 60 | 27 | 7 | 6 | | | | 93 | 7 | | | |
| W | <i>Lim. fletcheri</i> | 71 | 31 | 38 | 17 | 14 | 16 | 52 | 30 | 3 | | 32 | 48 | 14 | 4 | 1 | | | 89 | 3 | 9 | | |
| W | <i>Lim. salmini</i> | 8 | | 63 | 38 | | 38 | 38 | 25 | | | 75 | 25 | | | | | | 100 | | | | |
| W | <i>R. parinsignifera</i> | 13 | 46 | 23 | 23 | 8 | | 15 | 54 | 31 | | | 23 | 31 | 23 | 23 | | | 62 | 23 | 15 | | |
| C (end.) | <i>Lit. castanea</i> | 9 | 78 | 22 | | | | 11 | 33 | 44 | 11 | | 22 | 44 | 33 | | | | 78 | | 22 | | |
| R | <i>Lit. aurea</i> | 3 | | 67 | 33 | | | | 67 | 33 | | | 66 | | | 33 | | | 100 | | | | |
| R | <i>Lit. gracilentia</i> | 1 | 100 | | | | | | 100 | | | | 100 | | | | | | 100 | | | | |
| R | <i>Lit. nasuta</i> | 1 | 100 | | | | | | 100 | | | | 100 | | | | | | 100 | | | | |
| R (end.) | <i>Lit. piperata</i> | 5 | | 40 | 60 | | 20 | 40 | 40 | | | | | 80 | 20 | | | | 20 | | 80 | | |
| R | <i>Lit. tyleri</i> | 1 | | | 100 | | | | 100 | | | | | | | 100 | | | | | 100 | | |

TABLE 1 cont...

| Gp. | Species | July Min. C | | | | Elevation (m) | | | | | Rainfall (mm) | | | | | | | Vegetation | | | | | |
|-----|---------------------------|-------------|----|----|-----|---------------|----|-----|-----|----|---------------|-----|----|-----|----|----|----|------------|-----|----|-----|----|----|
| | | N | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 |
| R | <i>Lim. terraereginae</i> | 4 | 25 | 50 | 25 | | | 50 | 50 | | | 25 | 50 | | | 25 | | | 75 | | | | 25 |
| R | <i>Neo. sudelli</i> | 9 | 33 | 56 | 11 | | 11 | 11 | 78 | | | | 56 | 22 | 11 | | 11 | | 63 | 13 | 12 | 12 | |
| R | <i>Noto. bennettii</i> | 2 | 50 | 50 | | | | 50 | 50 | | | | 50 | 50 | | | | | 100 | | | | |
| R | <i>P. australis</i> | 1 | 33 | 34 | 33 | | | 33 | 34 | 33 | | 33 | 34 | | | | 33 | | 67 | | | | 33 |
| R | <i>P. major</i> | 1 | | | 100 | | | | 100 | | | | | 100 | | | | | | | 100 | | |
| R | <i>U. tyleri</i> | 1 | | | 100 | | | 100 | | | | 100 | | | | | | | 100 | | | | |

few records for this group lie in the lower environmental ranges.

Central species (Table 1, C) There is only one species in this category. *Litoria castanea*, which occupies a very limited area in the Guyra district. There is a 1958 record from near Armidale but there has been only one unsubstantiated record (1991) from Armidale since then. The few records of this species are concentrated at the low end of the temperature scale, the high end of the elevational scale and the middle range for rainfall. Its habitat lies in the predominantly DR + CL zone of a long established pastoral region. The closely related and more easterly *L. aurea* has a similar environmental profile except for higher midwinter minimal temperatures and a somewhat wider range of rainfall. *Litoria castanea* is also rare, endemic and perhaps extinct.

Endemic species (Table 1, end). Two species are endemic to New England, *L. castanea* (see above) and *L. piperata*. The latter species occupies wet forests in the higher rainfall zones at higher elevations along the eastern boundary of New England and may be considered a relictual species. It is greatly to be regretted that the survival of these two species is in serious doubt.

Rare Species (Table 1, R). These are species that were found too infrequently in the New England region to produce a meaningful distribution map. They may have restricted local distributions or it may be that they are more widely distributed but seldom found by collectors because they have secretive habits or for other reasons. They are *Litoria aurea*, *L. gracilenta*, *L. nasuta*, *L. tyleri*, *Limnodynastes terraereginae*, *Neobatrachus sudelli*, *Notaden bennettii*, *Pseudophryne australis*, *P. major* and *Uperoleia tyleri*.

Pseudophryne australis was reported by Cogger (1992) to occupy an area of only about 160km radius from Sydney and restricted to the Hawkesbury Sandstone formation. The New England records represent a considerable range ex-

tension; perhaps the species is more widespread than previously thought but rare in areas peripheral to the Sydney region. *Pseudophryne major* represents a small population restricted to Mt Kaputar in the extreme northwest of New England and well separated from the coastal population in Queensland. *Litoria aurea* is a widely distributed species. No explanation can be offered as to why it should be so restricted regionally. The record of *Litoria tyleri* presumably marks the western limit of this coastal species of northern New South Wales and southern Queensland. *Uperoleia tyleri* unexpectedly provides an inland record near Tamworth, well separated from the coastal population of southeastern New South Wales and Victoria.

This is a somewhat arbitrary grouping that shows as much or as little variation across environmental parameters as other groups. Despite small numbers of records the members of this group divide into those that are essentially eastern and those that are western.

CONCLUDING REMARKS

In summary, there is a number of species that meet their distributional limits within the New England area. Two of these are endemic to New England. Most are frogs either from moist habitats and which have distributions along the eastern coast and into the Great Dividing Range, and occur only in the eastern part of New England, or those adapted to the western arid plains and occurring only in the western part of the New England region. These two groups could almost be divided by a line running north and south through the region. There are a few species with generally northern or western distributions that just get into the northern edge of the study area. Superimposed on these is a large number of eurytopic, species that occur over wide areas of Australia and are found throughout New En-

TABLE 2. Systems of vegetation in New England. Data by courtesy of H. Hines, Armidale Branch National Parks & Wildlife Services, N.S.W.

| TYPE | AREA(ha) | % |
|-------------------------|-----------|--------|
| Disturbed remnant (DR) | 771,990 | 14.8 |
| Cleared (CL) | 2,600,384 | 53.3 |
| Rocky complex (RC) | 11,169 | 0.2 |
| Dry open forest (DF) | 1,105,702 | 22.7 |
| Woodland (WDL) | 45,295 | 0.9 |
| Moist open forest (MOF) | 153,294 | 3.1 |
| Rainforest (RF) | 29,762 | 0.6 |
| Unmapped | 40,469 | 0.8 |
| | 4,879,915 | 100.00 |

gland. A few species have range boundaries extending in all directions beyond those of New England but which have restricted distributions within the region. Finally, there is a group of species only recorded from a few, sometimes scattered, localities whose local distributions are hard to interpret; they may be rare or restricted to specialized local conditions or their apparent scarcity may be an artefact of collecting techniques. Ford & Macfarland (1991) recognised fifteen loose geographical categories for the birds of the New England region. It is interesting that these include the seven categories ascertained for the frogs.

ACKNOWLEDGEMENTS

There are many people who have contributed to this project over the more than 25 years it has been in progress. They include several generations of enthusiastic students, research assistants and technicians who participated in collecting and curatorial tasks. Many contributed sufficient time, effort and ideas that it would be appropriate to include them as authors were it not for the fact it would swell the authorship to unmanageable proportions. We hope they will recognise that our gratitude extends far beyond the inadequate token of this brief acknowledgment. They are: John Parmenter, Geoffrey Witten, John Veron, Bruce Firth, Malcolm Mackinnon, David Horton, Richard Shine, the late Malumo Simbotwe, Janet Taylor, Christopher Daniels, Carol Belmont, David Dye, John Overell, Sharon Fraser and Kenneth Zimmerman. Audry Heatwole, Eric Heatwole, Miguel Heatwole and Richard Moresley also helped collect specimens during the early part of the study. Many individuals from the local community, too numerous to mention, brought in

specimens. The study depended on the cooperation of the Australian Museum, the Queensland Museum and the Museum of Victoria in making available their herpetological registrations for the New England area and for the prompt response of the curatorial staff to queries about anomalous specimens, in particular Elizabeth Cameron, Jeanette Covacevich, Glen Ingram, Ross Sadlier, Patrick Couper and John Coventry. This paper was immensely facilitated by computer-generated distributional and environmental maps provided through the courtesy of Simon Ferrier and Harry Hines of the local office of the National Parks and Wildlife Service. We are very grateful for their kindness and patience. The map of *Litoria barringtonensis* derives from taxonomic determination by Michael Mahony. Karen Thumm advised concerning the status of *Pseudophryne australis* in New England and Marion Anstis concerning *L. barringtonensis*. Ivan Thornton of the Media Resource Unit, University of New England assembled the plates of distribution which were photographically reduced by Michael Roach of the Cartography section, who also prepared Figs 2-4. Our grateful thanks go to Sandy Hamdorf and Louise Percival for computer enhancement and labelling of all the figures. Our grateful thanks are extended to Jane Sefston for her patience and dedication in typing the final drafts. The Internal Research Funds of the University of New England provided partial support for several years and a grant from the Australian Biological Resources Study to H. Heatwole and A. F. O'Farrell financed it for 1976-1977. The rest of it depended on the generous, voluntary labour of the persons mentioned above. Our gratitude is extended to Hugh Ford and John Monro for critically commenting on the manuscript.

LITERATURE CITED

- BARKER, J. & GRIGG, G. 1977. 'A field guide to Australian frogs'. (Rigby Ltd.: Sydney).
 BROOK, A. J. 1977. ABIGS (Australian Biogeographical Integrated Grid System) Technical Manual, 1977 edition. (Department of Zoology, University of Melbourne: Parkville).
 COGGER, H. G. 1992. 'Reptiles and Amphibians of Australia'. (Reed: Sydney).
 COGGER, H. G., CAMERON, E. E. AND COGGER, H.M. 1983. 'Amphibia and Reptilia, Zoological Catalogue of Australia, Volume 1.' (Bureau of Flora and Fauna: Canberra).
 DAVIES, M. & LITTLEJOHN, M.J. 1986. Frogs of the genus *Uperoleia* Gray (Anura: Leptodactylidae) in south-eastern Australia. Transactions of the

- Royal Society of South Australia. 110(3-4) 111-143.
- FORD, H. A. & MACFARLAND, D. C. 1991. Faunal survey of New England. III. The birds. *Memoirs of the Queensland Museum* 30(3): 381-431.
- HEATWOLE, H. & SIMPSON, R. D. 1986. Faunal survey of New England. I. Introduction and general description of the area. *Memoirs of the Queensland Museum* 22(1): 107-113.
- INGRAM, G. J. & CORBEN, C. J. 1994. Two new species of broodfrogs (*Pseudophryne*) from Queensland. *Memoirs of the Queensland Museum* 37(1): 267-272.
- INGRAM, G. J., NATTRASS, A. E. O., CZECHURA, G. V. 1993. Common names for Queensland frogs. *Memoirs of the Queensland Museum* 33(1): 221-224.
- LEA, D. A. M., PIGRAM, J. J. & GREENWOOD, L. (eds) 1977. 'An atlas of New England. Vol. 1. The maps'. (Department of Geography, University of New England: Armidale).
- LITTLEJOHN, M. J. 1958. A new species of frog of the genus *Crinia* Tschudi from southeastern Australia. *Proceedings of the Linnaean Society of New South Wales* 83: 222-226.
- MARTIN, A. A. 1972. Studies in Australian Amphibia III. The *Limnodynastes dorsalis* complex (Anura: Leptodactylidae). *Australian Journal of Zoology* 20: 165-211.
- MARTIN, A. A., WATSON, G. F., GARTSIDE, D. F., LITTLEJOHN, M. J. & LOFTUS-HILLS, J. J. 1979. A new species of the *Litoria peronii* complex (Anura: Hylidae) from eastern Australia. *Proceedings of the Linnaean Society of New South Wales* 103: 23-25.
- MOORE, J. A. 1961. The frogs of eastern New South Wales. *Bulletin of the American Museum of Natural History* 121(3): 1-385.
- SIMPSON, R. D. & STANISIC, J. 1986. Faunal survey of New England. II. The distribution of gastropod molluscs. *Memoirs of the Queensland Museum* 22(1): 115-139.
- TYLER, M. J. 1992. 'Encyclopaedia of Australian Animals: Frogs'. Collins, Angus & Robertson (Australia) Pty. Ltd.: Sydney. 109pp.
- TYLER, M. J. & ANSTIS, M. 1975. Taxonomy and biology of the frogs of the *Litoria citropa* complex (Anura: Hylidae). *Records of the South Australian Museum* 17: 41-50.
- TYLER, M. J. & DAVIES, M. 1985. A new species of *Litoria* (Anura: Hylidae) from New South Wales, Australia. *Copeia* 1985(1): 1145-149.
- VAN BEURDEN, E. 1981. Bioclimatic limits to the spread of *Bufo marinus* in Australia: a baseline. *Proceedings of the Ecological Society of Australia* 11: 143-149.

APPENDIX

TABLE 1 Environmental Codes

| Code | July min. temp. (°C) | Code | Elevation (m) | Code | Rain (mm) | Code | Vegetational System |
|------|----------------------|------|---------------|------|-----------|------|-----------------------------|
| 1 | <0 | 1 | 0-399 | 1 | <700 | 1 | Disturbed remnant + cleared |
| 2 | 0-2 | 2 | 400-799 | 2 | 700-799 | 2 | Rocky complex |
| 3 | 2-4 | 3 | 800-1199 | 3 | 800-899 | 3 | Dry forest and woodland |
| 4 | 4-6 | 4 | 1200-1399 | 4 | 900-1099 | 4 | Moist open forest |
| | | 5 | >1400 | 5 | 1100-1299 | 5 | Rainforest |
| | | | | 6 | 1300-1499 | | |
| | | | | 7 | 1500-1699 | | |

TWO NEW SPECIES OF *POMADASYS* (PISCES: HAEMULIDAE) FROM OMAN, WITH
A REDESCRIPTION OF *P. PUNCTULATUS* (RÜPPELL)

ROLAND J. MCKAY AND JOHN E. RANDALL

McKay, R.J. & Randall, J.E. 1995 06 01: Two new species of *Pomadasys* (Pisces: Haemulidae) from Oman, with a redescription of *P. punctulatus* (Rüppell). *Memoirs of the Queensland Museum* 38(1): 251-255, Brisbane. ISSN 0079-8835.

Two new species of *Pomadasys* are described from Oman: *P. taeniatus*, distinctive in having seven dark brown stripes which do not bifurcate anteriorly, and *P. aheneus* with the dorsoanterior half or more of the body and postorbital head brassy yellow, fins grey with the soft portions of dorsal fin and caudal fin almost black. *Pomadasys punctulatus* (Rüppell, 1835), ranging from the Red Sea to Gulf of Oman is removed from synonymy and redescribed.

R.J. McKay, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; J.E. Randall, Bishop Museum, PO Box 1900A, Honolulu, Hawai'i 96817-0916, United States of America; 10 March 1995.

Recent collections of fishes from Oman by the junior author and associates resulted in specimens of three species of *Pomadasys* that could not be identified from the existing review literature of the family Haemulidae from the western Indian Ocean, including McKay (1984) and Smith & McKay (1986). One of the species, represented by specimens from the Gulf of Oman and southern Oman, proved to be *Pomadasys punctulatus* (Rüppell) which Fowler (1931) placed in the synonymy of *P. furcatus* (Bloch & Schneider). We here resurrect this species from synonymy and provide a redescription. The other two species are described as new to make the names available for a book on Oman fishes in preparation by the junior author and a FAO Species Catalogue of the family Haemulidae currently being written by the senior author.

Lengths given for specimens are standard length (SL), measured from tip of snout to base of caudal fin (hypural plate flexure); body depth is maximum depth from base of dorsal spines; head length is taken from tip of snout to posterior margin of opercular membrane; snout length is taken between verticals from tip of snout (not including lip) to fleshy margin of orbit; eye diameter is greatest width between fleshy margins of orbit; interorbital space is least fleshy width; pre-orbital depth is least depth of preorbital from lower edge of orbit to above end of maxilla or before; caudal peduncle depth is least depth. The last divided ray of the dorsal and anal fins is counted as $1\frac{1}{2}$; pectoral-ray counts include upper rudimentary ray; lateral-line scale counts are made to caudal flexure and do not include pored scales posterior to hypural plate; circumpeduncular scales are taken along one diagonal row from

above and below pored scale to pored scale on the other side, the upper count is given first, two pored scales and then lower count (total count is least number of scales around caudal peduncle); interradial scales are very small scales distal to basal sheath of scales into which base of dorsal and anal fins insert (magnification is sometimes required to locate these scales which are normally absent in this genus); gill-raker counts are made on first arch and include all rudiments that are at least as long as wide; upper count is given first; lower count includes raker at angle. Stripes are horizontal bands.

Data in parentheses in description refer to holotype.

Type specimens have been deposited in the Bernice P. Bishop Museum, Honolulu (BPBM); Naturhistorisches Museum Vienna (NMW); and Queensland Museum (QM).

Pomadasys aheneus sp. nov.
(Fig. 1A, B)

MATERIAL EXAMINED

HOLOTYPE: BPBM35931, 211mm SL, collected by handnet in 6m at Raysut Rock (16°56'1"N, 54°0'8"E), off Salalah Harbour, Oman, by J.L. Earle, 26 Oct 1993. PARATYPES: BPBM36055, three specimens 158, 165, 189mm SL, collected by spear in 8m at Raysut Rock by J.E. Randall, 08 Nov 1993. BPBM36166, 99 mm SL, collected by spear in 2m on rock and sand bottom on the east side of Masirah Island, Oman, by J.E. Randall, 20 Nov 1993. BPBM36161, 34mm SL, collected by handnet in 12m on the east side of Masirah Island, by J.L. Earle and J.E. Randall, 20 Nov 1993. QM29206, 183mm SL, collected by spear in 8m at base of breakwater at Raysut, by J.E. Randall, 08 Nov 1993.

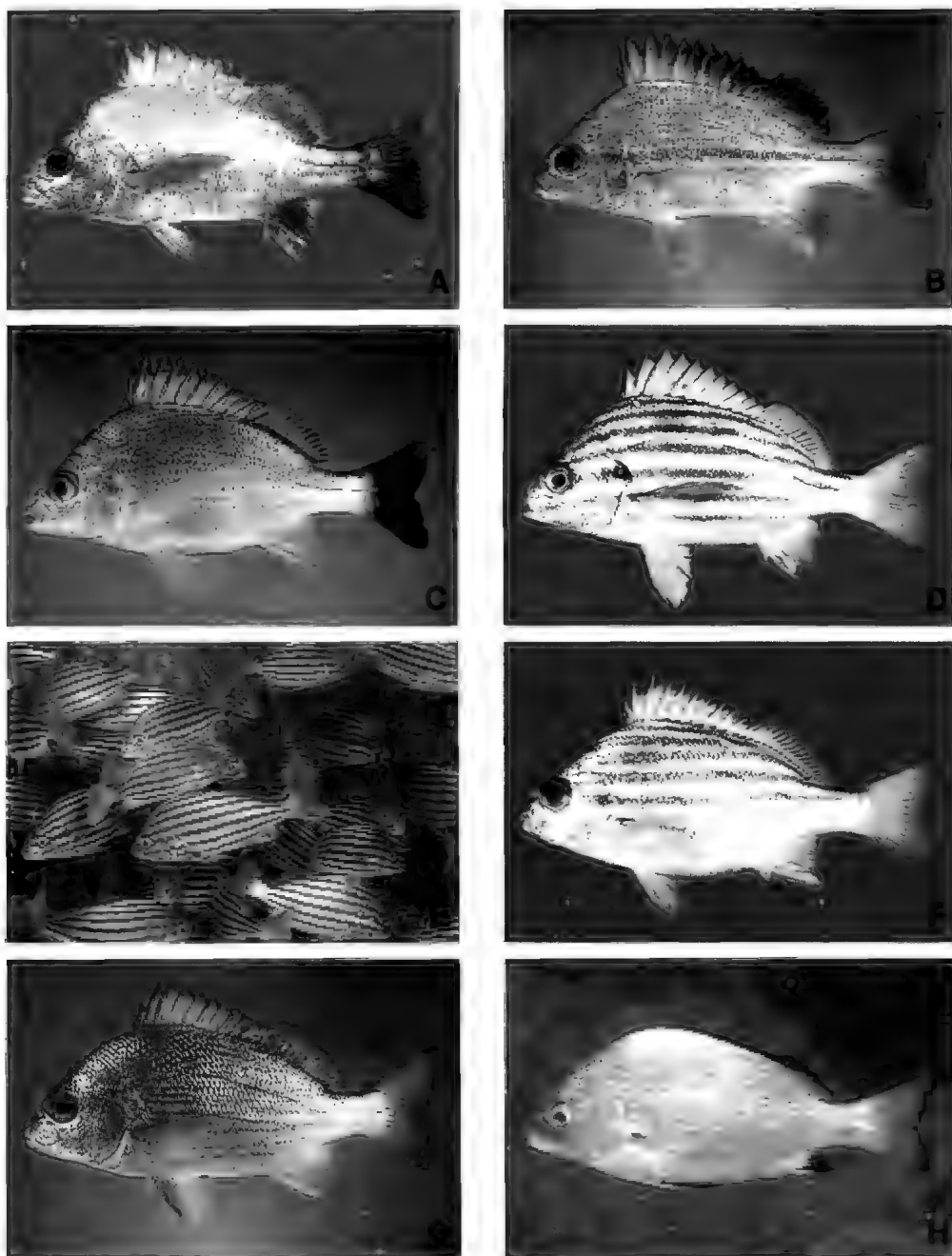


Fig. 1. A, B, *Pomadasys aheneus* sp nov. A, holotype, BPBM35931, 211mm SL, Raysut, S. Oman. B, paratype, BPBM33166, 99mm SL, Masirah Is., Oman. C, *Pomadasys guoraca*, BPBM19033, 167mm SL, Sri Lanka. D, E, *Pomadasys taeniatus* sp nov. D, paratype, BPBM35841, 140mm SL, Hoon's Bay, S. Oman. E, aggregation, southern Oman. F, *Pomadasys furcatus*, BPBM27724, 136mm SL, southern India. G, H, *Pomadasys punctulatus*. G, BPBM35944, 175mm SL, Mahalla, Oman. H, underwater photograph, southern Oman.

DIAGNOSIS

A small species of *Pomadasys* with one or two rows of small interradial scales on the dorsal and anal fins; 11 to 12 dorsal spines and $14\frac{1}{2}$ dorsal rays; anal fin with $8\frac{1}{2}$ rays; circumpeduncular scales 26; colour in life brassy yellow on nape, anterior part of back, and upper sides; caudal fin and most of rayed dorsal fin blackish; juveniles yellow with two well-defined brown horizontal stripes and a thinner brown stripe in between.

DESCRIPTION

Dorsal fin elements XI-XII, $14\frac{1}{2}$; anal fin elements III, $8\frac{1}{2}$; pectoral rays 17 (17 rarely 16; gill-rakers 5-6+12-13 (5+13); lateral line scales 51-53(52); circumpeduncular scales $11+2+13=26$. Body oblong, compressed, its depth (90mm) 41 to 44% of SL (211mm); dorsal profile straight; least depth of caudal peduncle (25mm) 11.7 to 13% of SL. Head (70mm) 33 or 34% of SL; snout rounded, length (18mm) 25 to 27%; fleshy interorbital space (21mm) 29 to 31%; width of preorbital (12.8mm) 18 to 19.5%; eye (16.5mm) 24 to 28% of head length; mouth small, terminal, without fleshy lips, posterior edge of upper jaw reaching to anterior margin of eye; upper and lower jaws with band of small conical teeth in about 7 rows anteriorly, outer row enlarged; palate without teeth; deep pore above maxilla under preorbital; gill-rakers short (about 3mm long, about equal to arch at angle); four pores on chin, posterior two slit-like, within deep conspicuous pit; preoperculum serrate, coarsely so at angle. Dorsal fin with third and fourth spines (33mm) longest; second anal spine (38mm) longer and stronger than third, all spines striated; caudal fin slightly forked; soft portions of dorsal and anal fins with two or three proximal and one to two distal rows of interradial scales; basal sheath of scales present; $8\frac{1}{2}$ or $9\frac{1}{2}$ ($8\frac{1}{2}$) rows of scales in oblique line between origin of dorsal fin and lateral line.

Colour. In life, juveniles yellow with dark brown horizontal stripe originating on interorbital space and continuing posteriorly just below spinous dorsal fin and running just below rayed dorsal fin to upper origin of caudal fin, thin brown stripe from upper eye to middle of body along lateral line and distinct black-brown stripe from behind middle of eye to middle of caudal fin base where it terminates in black-brown confluent spot, fins yellow; at 99mm SL the coloration brassy yellow on nape, and anterior part of back and upper sides, with well-defined horizontal dark brown to blackish stripe behind eye to mid-

dle of caudal fin, four or five indistinct thin dark stripes above, and very indistinct thin dark stripe below from origin of pectoral fin to above posterior part of anal fin; distal half of dorsal fins blackish; caudal fin dusky; anal rays dusky; and pelvic fin rays olive; adults with anterior part of body and upper sides brassy to golden; outer tips of spinous dorsal fin dark brown to black, most of rayed dorsal and caudal fin black; anal and pelvic fins dusky, second anal spine darker. In alcohol, the brassy coloration is pale brown. Swimbladder simple without anteriolateral horn-like extensions.

ETYMOLOGY

From the latin *aeneus* or *aheneus* meaning bronze or brassy in reference to the characteristic brassy yellow anterodorsal coloration of this species in life.

REMARKS

Very similar to *Pomadasys guoraca* (Cuvier, 1830) from India and Sri Lanka, (see Fig. 1C) but with $8\frac{1}{2}$ anal rays, 26 circumpeduncular scales (11 above, 2 pored and 13 below) and coloration brassy on anterior back, upper sides and nape, caudal fin and soft dorsal fin blackish. *P. guoraca* (Plate 1D) has $7\frac{1}{2}$ anal rays, 22 circumpeduncular scales ($9+2+11$), and is silvery with yellow horizontal stripes following scale rows below lateral line, of which four or five are distinct; caudal fin dusky to black with a posterior white margin; soft dorsal fin pale with dark base; anal and paired fins bright yellow.

Pomadasys taeniatus sp. nov.

(Fig. 1D, E)

Pomadasys furcatus (non Bloch & Schneider): Steindachner, 1907:130 (Gischin, South Arabia = Qischin, Yemen)

MATERIAL EXAMINED

HOLOTYPE: BPBM35841, 140mm SL, collected by spear in 3m at Hoon's Bay ($16^{\circ}58'0''N$, $54^{\circ}42'50''E$), Oman, by J.E. Randall, 23 April 1990. Colour photograph of holotype.

PARATYPES: National Museum Vienna NMW38942: 1-2, two specimens, 128mm, 141mm SL, collected at Gischin by Hein, 14 Apr 1902; specimens reported as *P. furcatus* by Steindachner, 1907).

DIAGNOSIS

A small species of *Pomadasys* with one or two rows of small interradial scales on dorsal and anal fins; 12 dorsal spines and $15\frac{1}{2}$ dorsal rays; anal

fin with $8\frac{1}{2}$ rays; circumpeduncular scales 26; colour in life silvery with seven undivided dark bronze stripes.

DESCRIPTION

Dorsal fin elements XII, $15\frac{1}{2}$; anal fin elements III, $8\frac{1}{2}$; pectoral rays 17, rarely 16 (17); gillrakers 5-6+12 (6+12); lateral line scales 52-53 (52); circumpeduncular scales $11+2+13=26$. Body oblong, compressed, its depth (60mm) 42 to 43% of SL (140mm); dorsal profile straight; least depth of caudal peduncle (16.8mm) 11.7 to 12.3% of SL. Head (46.3mm) 32 to 33% of SL; snout rounded, length (12mm) 26 to 27%; fleshy interorbital space (14mm) 30 to 31%; width of preorbital (9mm) 19 to 21%; eye (11.8mm) 24 to 26% of head length; mouth small, terminal, without fleshy lips, posterior edge of upper jaw reaching to anterior margin of eye; upper and lower jaws with band of small conical teeth in about 7 rows anteriorly, outer row enlarged; palate without teeth; shallow pore above maxilla under preorbital; gillrakers short (about 2.5mm long, about equal to arch at angle); preoperculum serrate, coarsely so at angle. Dorsal fin with third and fourth dorsal spines (24mm) longest; second anal spine (23mm) longer and stronger than third, all spines striated anteriorly; soft portions of dorsal and anal fins with one or two proximal and one distal row of interradial scales; basal sheath of scales present; $7\frac{1}{2}$ or $8\frac{1}{2}$ ($8\frac{1}{2}$) rows of scales in oblique line between origin of dorsal fin and lateral line.

Colour: in life, body silvery with seven dark bronze stripes which converge without bifurcating onto head; a blackish spot posteriorly on opercle superimposed on fifth bronze stripe and extending a little above; fins purplish-grey except basal three-fourths of spinous part of dorsal fin which is whitish and scaly sheath at base of anal fin which is silvery. In alcohol, body pale brown with seven distinct undivided dark brown stripes each about one to one-and-a-quarter scales in width separated by about one and one-half scales; uppermost curved stripe originates on nape and runs along base of spinous dorsal fin, extending onto base of interspinous membranes and along base of rayed dorsal fin; second curves up from nape and terminates at middle of rayed dorsal fin base; third from above eye and lateral line to run along posterior third of rayed dorsal fin; fourth is almost straight from above eye onto origin of lateral line, thence below to just before level of posterior dorsal spines where it crosses lateral line again to continue just below dorsal surface of

caudal peduncle; fifth from behind middle of eye through dark brown blotch on upper part of opercle to middle of caudal peduncle; sixth from below eye to upper pectoral base and along side to lower part of caudal peduncle; seventh from below pectoral fin base to fade above end of anal fin base; thin poorly defined eighth stripe from bottom of opercle, between pelvic and pectoral base to above rayed anal fin where it broadens to cover most of scaly sheath of anal fin; dorsal fin with interspinous membranes indistinctly blotched between third to seventh spines; other fins slightly dusky. Swimbladder simple without anteriolateral horn-like extensions.

ETYMOLOGY

From the Latin *taenia* meaning ribbon or band.

REMARKS

Very similar to *Pomadasys furcatus* (Bloch & Schneider, 1801), (see Fig. 1F) but with seven or eight undivided dark brown longitudinal stripes. The juvenile of the former species may have the stripes undivided, but by 100mm SL second, third and fourth stripes are bifurcate at least anteriorly; adults have second, third and fourth stripes bifurcate to about fifth dorsal spine and fifth stripe bifurcate on opercle; sixth stripe usually undivided. Specimens of 225mm SL have upper stripes divided to about the vertical from sixth dorsal spine.

The new species has the dark stripes well defined, without trace of anterior division. The interradial membranes of the soft dorsal fin have one or two rows of scales as does *P. furcatus*. Recent illustrations of *P. furcatus* are given by Gloerfelt-Tarp & Kailola (1984:198), McKay (1984), Smith & McKay, (1986: 179,11).

Related to *Pomadasys andamanensis* with four distinct undivided black-brown stripes recently found in the Andaman Sea (McKay & Satapoomin, 1994).

Pomadasys punctulatus (Rüppell, 1838) (Fig. 1G, H)

Pristipoma punctulatum Rüppell, 1838: 124, pl. 30 fig. 3 (type locality Massaua, Red Sea).

MATERIAL EXAMINED

BPBM21425 (2), 204mm, 205mm SL, Gulf of Oman, fish market at Port Qaboos, Matrah, Oman. BPBM35944, 176mm SL, Mahallah, southern Oman. NMW38943 (2), 76mm, 94mm SL, Gischin, 1902, collected Hein (reported by Steindachner, 1907).

DESCRIPTION

Dorsal fin elements XII, 15½; anal fin elements III, 8½; pectoral rays 16; gillrakers 5-6+12-13; lateral-line scales 50-52; circumpeduncular scales 9-10+2+11-13=22-25. Body oblong, compressed, its depth 40 to 44% of SL. Head 31 to 33% of SL; snout 23 to 27%; eye 24 to 25% of head length (decreases with growth); mouth small, terminal, without fleshy lips, posterior edge of upper jaw reaching to anterior margin of eye; deep pore above maxilla under preorbital well developed in juveniles, moderate in large adults; preoperculum finely serrate; second anal spine longer and stronger than third, all spines longitudinally striated; soft portions of dorsal and anal fins with row of interradial scales; basal sheath of scales present; pectoral fins 35 to 37% of standard length, reaches to or just beyond anus; 8 to 10 rows of scales in oblique line between origin of dorsal fin and lateral line, 7½ scales above lateral line at middle of spinous dorsal fin.

Colour: In life, silvery, the back with faint yellow-green iridescence, with irregular narrow brown stripes on upper two-thirds of body; fins dusky, caudal fin darkest; faint dark spots in a row at base of dorsal fin; large diffuse blackish blotch on membranes anteriorly in middle of pelvic fins; mouth with palate and part of sides of mouth dull orange-red. In alcohol, body pale brownish, lighter below, back with 11 or 12 longitudinal brown lines on alternate scale rows, the upper ones broken into groups of small contiguous spots; dorsal fin with darker basal blotches on interspinous membranes and about two rows of spots on interradial membranes; juveniles with wavy longitudinal brown lines formed largely of contiguous spots; anal and pelvic fins pale yellowish; no dark spot on operculum. Swimbladder without anteriolateral horn-like extensions.

REMARKS

This species was placed in the synonymy of *P. furcatus* by Fowler (1931). It has a very distinctive colour pattern quite unlike the former species and generally has fewer lateral-line scales (50-52 v 52-54) and upper peduncular scales (9-10 v 11). Rüppell's figure is very accurate, but may have led Fowler to consider *P. punctulatus* as the adult of *P. furcatus* as the number of stripes increase with growth. However, we have examined small specimens of both species and the juvenile *P.*

punctulatus has the same pattern of thin stripes as the adult.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of Dr. Barbara Herzig of the Naturhistorisches Museum, Vienna, in forwarding specimens for study, Dr. Marie Louise Bauchot of the Museum national d'Histoire naturelle, Paris, provided considerable assistance when the first author studied type specimens of the family Haemulidae at the MNHN. John L. Earle assisted in collecting specimens.

LITERATURE CITED

- FOWLER, H.W. 1931. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the families Pseudochromidae, Lobotidae, Pempheridae, Priacanthidae, Lutjanidae, Pomadasysidae and Teraponidae, collected by the United States Bureau of Fisheries steamer "Albatross" chiefly in Philippine Seas and adjacent waters. Bulletin of the United States National Museum, 100(11):1-388, 29 figs.
- GLOERFELT-TARP, T. & KAILOLA, P. 1984. Trawled Fishes of Southern Indonesia and North-western Australia. (The Australian Development Assistance Bureau; The Directorate General of Fisheries, Indonesia; The German Agency for Technical Cooperation).
- McKAY, R.J. 1984. Pp. var. In Fischer, W. and Bianchi, G. (eds), FAO species identification sheets for fishery purposes. Western Indian Ocean; vol. 2 (Fishing Area 51). Prepared and printed with the support of the Danish International Development Agency (DANIDA). (Food and Agriculture Organization of the United Nations; Rome).
- McKAY, R.J. & SATAPOOMIN, U. 1994. *Pomadasys andamanensis*, a new species of haemulid fish from Thailand. Bulletin of the Phuket Marine Research Centre, 59: 1-4.
- RÜPPELL, E. 1838. Fische des rothen Meers. In: Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Frankfurt am Main. (1835: 1-28 pp, 1-7 pls; 1836: 22-52 pp, 8-14 pls; 1837: 53-80 pp, 15-21 pls; 1838: 81-148 pp, 22-33 pls.).
- SMITH, M.M. & McKAY, R.J. 1986. Pp. 564-571. In Smith, M.M. and Heemstra, P.C. Smith's Sea Fishes. (Macmillan South Africa: Braamfontein, Johannesburg).
- STEINDACHNER, F. 1907. Fische aus Südarabien und Sokotra. Denkschriften der Akademie der Wissenschaften, Wien. 71(1):123-168.

A MIDDLE JURASSIC FLORA FROM THE WALLOON COAL MEASURES, MUTDAPILLY, QUEENSLAND, AUSTRALIA

STEPHEN McLOUGHLIN AND ANDREW N. DRINNAN

McLoughlin, S. & Drinnan, A. N. 1995 06 01: A Middle Jurassic flora from the Walloon Coal Measures, Mutdapilly, Queensland, Australia. *Memoirs of the Queensland Museum* 38(1): 257-272. ISSN 0079-8835

A Middle Jurassic impression flora from the Walloon Coal Measures near Mutdapilly in the Clarence-Moreton Basin, Queensland, comprises one equisetalean species, four species of ferns, and one species each of pentoxylalean, probable conifer, and possible bennettitalean foliage. The assemblage also contains a large number of *Palisya ovalis* cones of uncertain systematic affinity. The assemblage is similar to other fossil suites from the Walloon Coal Measures, but has fewer conifer and bennettitalean remains. It is most closely comparable to the flora of the Clent Hills Group (Bajocian-Bathonian) of New Zealand. □ *Middle Jurassic, fossil macroflora, Walloon Coal Measures, Clarence-Moreton Basin, sphenophytes, pteridophytes, Pentoxylaes, conifers.*

Stephen McLoughlin and Andrew N. Drinnan: School of Botany, University of Melbourne, Parkville, Victoria 3052, Australia; 10 January 1995.

The Middle Jurassic flora of the Walloon Coal Measures is represented in coals (generally up to 2m thick) and interseam sediments. These coals have been exploited for over a century as a source of high volatile bituminous steaming coals (Fielding, 1993). Partial breakdown of the fossilized organic matter may also represent a potential source of liquid and gaseous hydrocarbons in deeper parts of the Surat and Clarence-Moreton Basins. Several palaeobotanical studies of the Walloon Coal Measures (notably Walkom, 1917; Gould, 1974, 1980; Rigby, 1978) have established the general composition of the flora. Gould (1974) provided a comprehensive list of previous palaeontological investigations of the coal measures. This study is intended to illustrate and describe a small assemblage of pteridophytic and gymnospermous taxa that occur as well-preserved impressions collected from a road cutting near Mutdapilly, southwest of Ipswich, Queensland. The Walloon Coal Measures flora is compared with several other Gondwanan Mesozoic fossil suites and its palaeoenvironmental implications are briefly considered.

GEOLOGICAL SETTING

The Walloon Coal Measures of the Clarence-Moreton Basin consist of interbedded volcanolithic sandstone, coal, mudstone, and siltstone, reaching a maximum thickness of about 250m (Exon et al., 1974; Cranfield et al., 1976). They conformably and gradationally overlie the Lower Jurassic Marburg Formation (dominated by quartzo-feldspathic sandstones) throughout

much of the basin and are conformably or disconformably overlain by the ?Middle Jurassic to ?Lower Cretaceous Woodenbong Beds in the southern Clarence-Moreton Basin. The coal measures are locally overlain unconformably by Tertiary and Quaternary sediments and volcanics in the northern part of the Basin (Fig. 1). The coal measures extend into the eastern part of the adjacent Surat Basin and correlate with the Birkhead Formation in the western Surat and Eromanga Basins and with coal-rich units in the neighbouring Mulgildie (Mulgildie Coal Measures) and Maryborough (Tiara Coal Measures) Basins. The Walloon Coal Measures palynoflora indicates a Middle Jurassic age (de Jersey, 1960; de Jersey & Paten, 1964; Burger, in Exon et al., 1974). Turner & Rozefelds (1987) recorded specimens of an actinopterygian fish from these strata. Dinosaur tracks are the only other fossils recorded from this unit (Bartholomai, 1966; Gould, 1974; Molnar, 1991).

Fielding (1993) identified seven sedimentary facies and three facies associations within the Walloon Coal Measures in the Rosewood-Walloon Coalfield. The facies associations are representative of major channel, floodbasin, and mire environments within a broad alluvial plain depositional setting. Limited palaeocurrent data suggested that streams in the northern Clarence-Moreton Basin generally drained in a southeasterly direction (Fielding, 1993). The Mutdapilly fossil plant assemblage was recovered from a roadcut at grid reference 692781 7465500 on the Ipswich 1:100 000 geological map (sheet 9442), (University of Queensland locality 5208) (Fig. 1).

The collection site is now obscured from view by groundcover vegetation and the Cunningham Highway.

MATERIAL AND METHODS

All specimens examined in this study are housed in the palaeontological collections of the Department of Earth Sciences, The University of Queensland, and are prefixed 'UQF'. The specimens were collected in the late 1980s from roadworks along the Cunningham Highway near Mutdapilly southwest of Ipswich, Queensland. The fossils are preserved as brown iron-stained impressions in yellow-grey shale and siltstone. No organic matter is preserved, preventing assessment of cuticular details. Forty-three slabs were considered in detail during this study; additional unfigured material is housed at the University of Queensland.

SYSTEMATIC PALAEOBOTANY

Phylum SPHENOPHYTA
Class SPHENOPSIDA
Order EQUISETALES
Family EQUISETACEAE

Equisetum Linnaeus, 1753
Equisetum bryanii Gould, 1968
(Fig. 2A, B)

MATERIAL EXAMINED
UQF79683, UQF79728.

DESCRIPTION

Incomplete segmented axes reaching in excess of 125mm long, width of flattened axis up to 8.5 mm. Axis more or less constant in width throughout with fine longitudinal striae, partitioned by transverse nodes 19-24mm apart (Fig. 2B). Whorl of elongate tooth-like flanged leaves surrounds each node (Fig. 2A). Around six leaves evident across stem impression (counterparts not available). Leaves closely adpressed to stem, extending 7-8mm distally beyond node, separated for 3-4mm below node. Leaves fused into a basal sheath tightly adpressed to axis and connected to stem at preceding (proximal) node. Leaf flanges continuous from base of sheath incision to apex. Midribs poorly defined. Fructifications and cuticular details unavailable.

COMPARISON AND REMARKS

Despite the absence of fertile material or cuticular detail, the described axes are assigned to *Equisetum* Linnaeus rather than *Equisetites* Sternberg following the conclusion of Harris (1961) and Gould (1968) that these genera are inseparable. The Mutdapilly specimens are readily referable to *E. bryanii* Gould by their smooth leaf sheaths and flanged, adpressed, free leaves with indistinct midribs. Specimens identified as *Equisetites approximatus* Halle 1913 from the mid- to late Mesozoic of the Antarctic Peninsula also show adpressed flanged leaves united into a long sheath and may be synonymous with *E. bryanii*. The absence of cuticular details and nodal diaphragms preserved in dorso-ventral view prevent detailed comparison to *Equisetum laterale* Gould 1974 but the latter can be distinguished by its more abruptly pointed leaves.

The Mutdapilly specimens are morphologically similar to extant *Equisetum* species and they probably occupied a similar ecological niche to extant species.

Phylum PTERIDOPHYTA
Class FILICOPSIDA
Order OSMUNDALES
Family OSMUNDACEAE

Cladophlebis Brongniart, 1828
Cladophlebis australis (Morris) Seward, 1904
(Figs 2C-F, 3A-D, G)

MATERIAL EXAMINED

UQF79680, UQF79681, UQF79684, UQF79686,
UQF79688-UQF79691, UQF79694, UQF79700,
UQF79704-UQF79706, UQF79723, UQF79729-
UQF79733, UQF79736.

DESCRIPTION

Fronds at least bipinnate (Fig. 2C,F) reaching in excess of 135mm long, 160mm wide. Rachis reaching at least 5mm wide, tapering distally, smooth or longitudinally striate. Pinnae dimorphic (either fertile or vegetative). Vegetative pinnae lanceolate or falcate reaching 90mm long, 26mm wide, alternate to opposite (Fig. 2C,F), catadromous, rachilla departing rachis at 30°-65°. Pinnules subopposite, ovate or lanceolate (Figs 2E; 3A,C) and commonly arched distally (falcate) reaching 17mm long, 6mm wide, margin entire or slightly serrulate, apex pointed acute, acroscopic margin of pinna base slightly obcurrent joined with basiscopic margin of adjacent pinnule base. Pinnule midveins depart rachilla at 40°-70°; lateral veins bifurcate once or twice

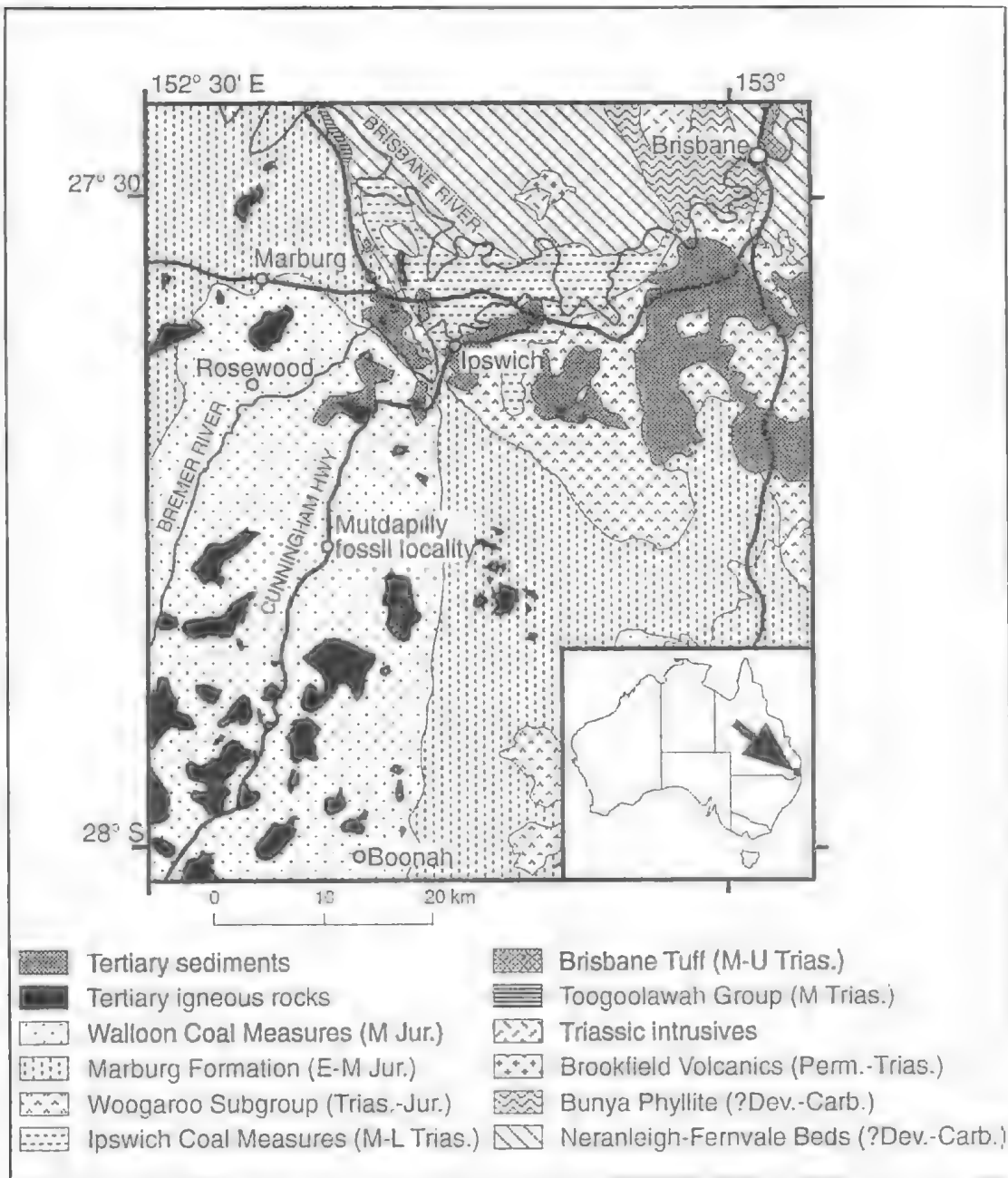


FIG. 1. Geological map of the Brisbane-Boonah district, southeast Queensland, showing location of the fossil locality at Mutdapilly, after Cranfield et al. (1976).

across the lamina. Sori or sporangia elliptical (0.4 x 0.5 mm), striate, borne in clusters of 4-6 at the ends of veins on the abaxial surface of modified (fertile) pinnules (Figs 2D; 3G). Fertile pinnules equivalent in dimensions (or slightly narrower) and in arrangement to vegetative pinnules but

often flexed distally (Fig. 3D), lamina surface is slightly undulate, margin slightly incised (incisions < 1 mm) between lateral veins which do not bifurcate. Spores and cuticular details are not available on these specimens.

COMPARISON AND REMARKS

Cladophlebis australis (Morris) Seward 1904 is one of the most widespread and abundant plant species in Australian Jurassic assemblages (Gould, 1975). There is considerable variation in size and shape of the pinnules amongst the Mutdapilly specimens (Figs 2E; 3A,C). Such morphological variants from individual localities have occasionally been assigned to a large number of species (e.g., see Halle, 1913) on inadequate criteria. Fronds and detached pinnae of *C. australis* are the most common plant remains in the Mutdapilly assemblage. It is not clear from the available material whether both fertile and sterile pinnae were attached to the same fronds. Fertile pinnae in the assemblage are either dispersed individually (Figs 2D; 3D,G) or attached to short rachis fragments (Fig. 3B). However, Walkom (1917: text-fig. 1) illustrated a fertile pinna of this species in which only the proximal pinnules were fertile.

Cladophlebis fronds have previously yielded sporangia containing osmundaceous spores (e.g., Harris, 1961) and the occurrence of abundant permineralized osmundaceous axes elsewhere in the Walloon Coal Measures, the similar shapes of the *C. australis* and *Osmundacaulis* petioles, and the clustered occurrence of some *Cladophlebis* fronds, strongly favours an osmundaceous affinity for *Cladophlebis australis* (Gould, 1973, 1974, 1980). The fertile pinnae described here show strong similarities to the osmundaceous fructification *Cacumen expansa* Cantrill & Webb 1987, which is probably affiliated with *Phyllopteroides* foliage. However, the Mutdapilly fertile pinnules appear to be bilaterally symmetrical with ranks of alternating sporangial clusters inserted on the abaxial surface either side of the midrib (Figs 2D; 3D,G) in contrast to the interpretation of *Cacumen* as bearing sporangia in radial arrangement about a reduced stalk-like pinna proposed by Cantrill & Webb (1987). Similar sporangial arrangements to those suggested for the Mutdapilly fronds are evident on cladophlebid pinnae from the Australian and South African Triassic (Walkom, 1917, text-fig. 1; Anderson & Anderson, 1983, pl. 5, fig. 4; pl. 6, figs 4, 5).

Cladophlebis sp. A
(Fig. 3E, F)

MATERIAL EXAMINED
UQF79679.

DESCRIPTION

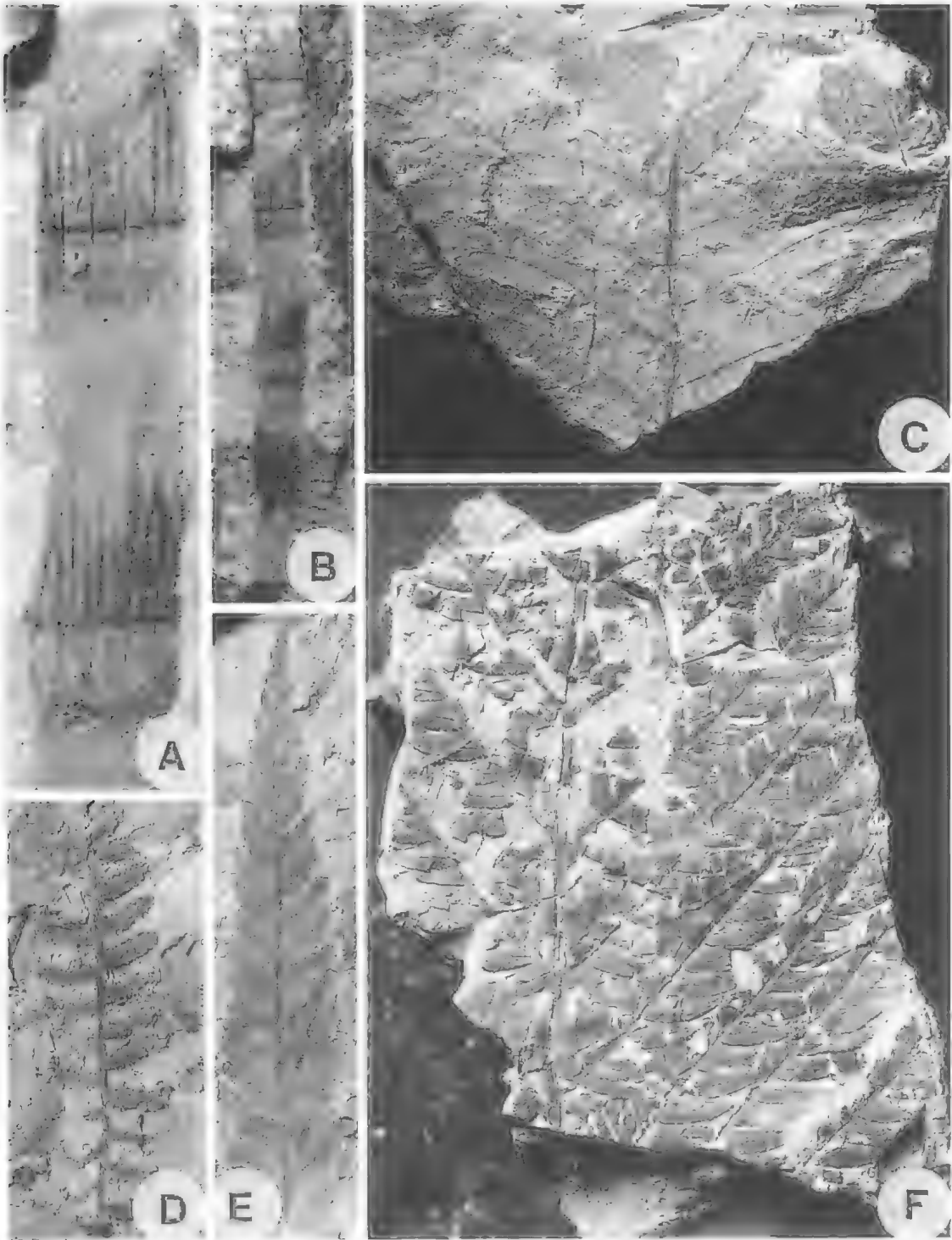
Frond at least pinnate, >5cm long, 2.5cm wide. Rachis 1mm wide at base of preserved frond, gently tapering distally. Pinnules ovate, decurrent, joined basally, subopposite, reaching 15mm long, 6mm wide. Pinnule margins lobed (Fig. 3E, F), apex rounded to pointed acute. Pinnule midribs prominent, slightly sinuous, arched sharply near base then passing along pinnule at 70°-80°, persistent. Pinnule venation basiscopic, lateral veins given off alternately at c. 40°-50° dichotomize once before margin, each vein pair entering a single marginal lobe (Fig. 3F). Cuticular details and fructifications unavailable.

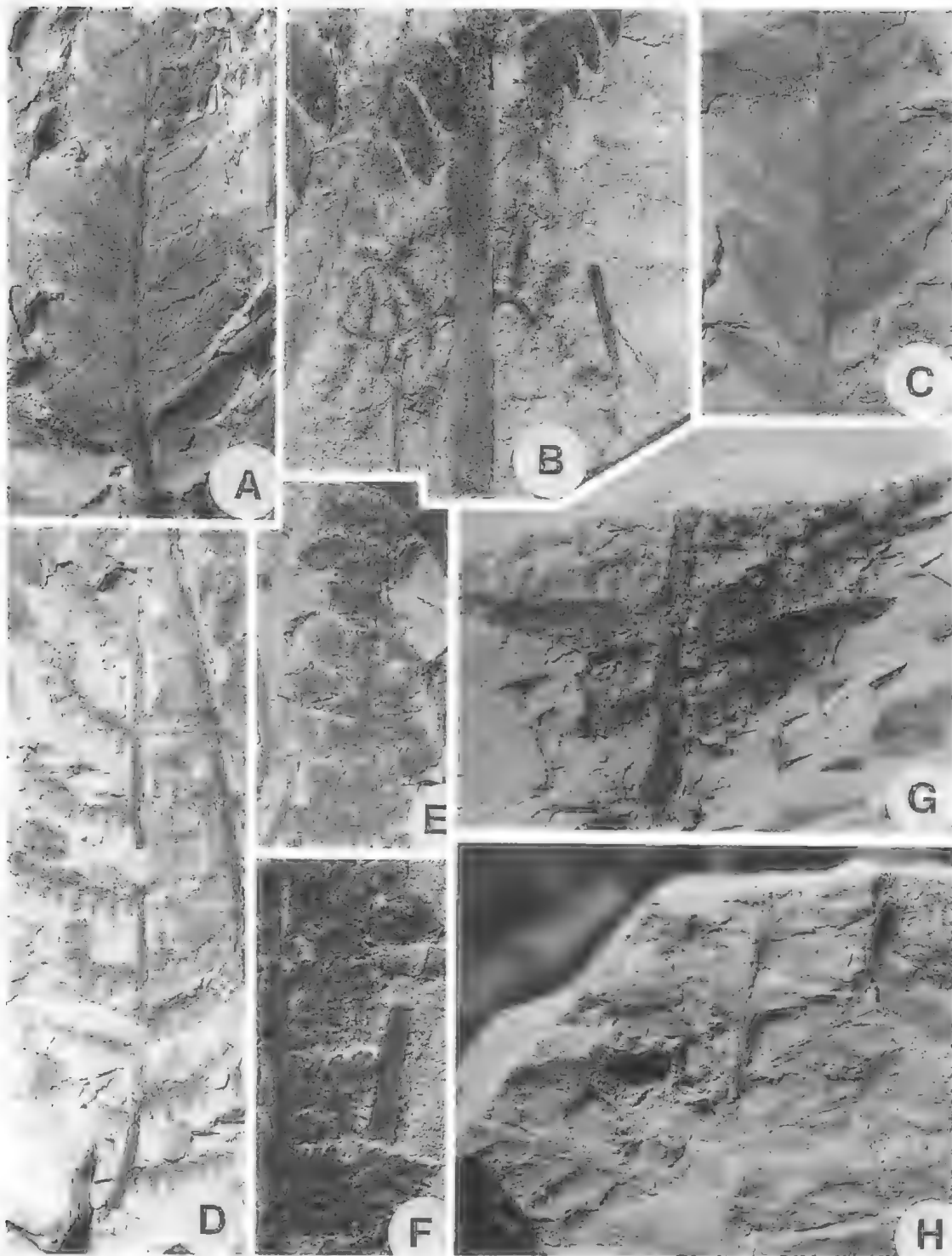
COMPARISON AND REMARKS

Although only a single incomplete frond (with counterpart) of this species is available it is readily distinguished from *Cladophlebis australis* by its lobed pinnules each incorporating two ultimate veins. The prominence of the lateral veins together with inter-vein arching of the lamina imparts a crenulate appearance to the pinnules. These features distinguish this specimen from all other cladophlebid fronds previously described from the Australian Mesozoic. Fertile pinnules of *C. australis* are sometimes crenulate or irregularly lobed but they differ from *Cladophlebis* sp. A by their more slender and falcate shape and less distinct venation.

Cladophlebis kathiawarensis Roy 1968 is the most closely comparable Indian fern with pointed serrate pinnules. Although each serration on *C. kathiawarensis* pinnules incorporates two veins, the marginal cusps are strongly inclined, more sharply pointed, and not as deeply incised as the pinnule lobes on *Cladophlebis* sp. A. Herbst (1971) reviewed the Argentinian species of *Cladophlebis* and noted that only *C. mendozaensis* (Geinitz) Frenguelli possessed dissected pinnule margins that are gently undulate rather than distinctly lobed.

FIG. 2. A, B, *Equisetum bryanii* Gould, 1968, showing sheaths of partly fused lanceolate leaves around each node, UQF79683, A x 3, B x 1. C-F: *Cladophlebis australis* (Morris) Seward 1904. C, bipinnate frond with alternate pinnae, UQF79681, x 0.5. D, fertile pinna, UQF79728, x 1. E, sterile pinna showing variation in pinnule size, UQF79732, x 1.5. F, bipinnate frond with opposite to sub-opposite pinnae, UQF79700, x 1.





Order FILICALES
Family DIPTERIDACEAE

Hausmannia Dunker, 1846
Hausmannia sp. cf. *H. deferrariisii*
Feruglio, 1937
(Fig. 4A-D)

cf. *Hausmannia Buchii* (?) (Andrae), Walkom, 1917: 11; text-fig. 4.

Hausmannia (*Protorhipis*) sp. Hill, Playford, & Woods, 1966: pl. J1, fig. 9.

Hausmannia sp. cf. *H. (Protorhipis) deferrariisii* Feruglio, Gould, 1974: 35 (no figs).

Hausmannia (*Protorhipis*) sp. cf. *H. (P.) deferrariisii* Feruglio, Herbst, 1979: 18, figs. 4.12, 4.13, 6.13, 6.14; non fig. 1.6; Gould, 1980: 93, figs 6, 15.

MATERIAL EXAMINED

UQF79672-UQF79677, UQF79687, UQF79692, UQF79693.

DESCRIPTION

Fronds broadly reniform (auriculate) with a medial distal notch, auricles sometimes nearly touching (though never fused) to give a bi-lobed circular to peltate appearance to the frond (Fig. 4B-D). Petiole (rachis) attachment in centre of frond lamina. Lamina reaching 117mm wide, 45mm from distal margin to petiole insertion, 31mm from petiole insertion to proximal margin of auricles. Distal medial cleft up to 15mm deep. Lamina symmetrical about the plane from petiole insertion to distal cleft. Petiole >17mm long, reaching at least 3 mm wide at connection with lamina. Petiole midvein bifurcates at base of lamina giving off a vein to each half of lamina. Each daughter vein then bifurcates up to seven times across lamina producing a radial array of tuning fork shaped principal veins which evanesce 2-5mm from margin (Fig. 4A,D). At least three further orders of subsidiary veins divide the intervening lamina into polygonal meshes. Apart from medial distal cleft, lamina margin entire or gently undulate with short (<2mm) notches between principal vein groups (Fig. 4A,D). Marginal vein present <0.2mm wide.

COMPARISON AND REMARKS

Mutdapilly fronds vary in size but show a consistently bi-lobed reniform shape. The relatively thick petiole attached to one specimen is also a feature that may be taxonomically important.

Herbst (1979) reviewed the previously described and illustrated Australian specimens of *Hausmannia* and concluded that three species (viz., *H. wilkinsii* Walkom, *H. sp. cf. H. deferrariisii* Feruglio, and *H. bulbiformis* Douglas) remained valid. *Hausmannia bulbiformis*, established for two specimens from the Victorian Early Cretaceous (Douglas, 1969), differs from the material described here by its more flabellate rather than reniform shape and its more dissected margin. *Hausmannia wilkinsii* can also be differentiated by its strongly dissected fronds (Walkom, 1928, Herbst, 1979). Herbst (1979) included both Middle Jurassic and Early Cretaceous forms within *Hausmannia sp. cf. H. deferrariisii*. However, the Early Cretaceous fronds from Western Australia and the Northern Territory illustrated by White (1961a, 1961b, 1966), now supplemented by better material housed in the Western Australian Museum, do not show the auriculate base characteristic of the Queensland Jurassic representatives of this species and should be transferred to a separate species.

Hausmannia papilio Feruglio from Argentina typically has a truncate base (Longobucco et al., 1985), but some examples illustrated by Herbst (1960) have a rounded auriculate base not dissimilar to the Mutdapilly specimens. Fertile material is not available in the Queensland assemblage preventing closer comparison to the Argentinian forms. *Hausmannia cf. nariwaensis* Oishi from the Hope and Botany Bay floras (Rees, 1993) of the Antarctic Peninsula differs from the Mutdapilly species by its greater length:width ratio and more prominently crenulate margins.

Hausmannia pachyderma Sukh-Dev 1971 and specimens assigned to *Hausmannia crenata* (Nathorst) Möller from India (Bose & Sah, 1968) do not show the strongly auriculate base or the deep apical cleft of the Mutdapilly specimens. The Indian *H. crookshanki* Shah & Singh 1964 is similar in shape to *H. sp. cf. H. deferrariisii* but differs in being substantially smaller with fewer principal veins which do not bifurcate as often across the lamina.

FIG. 3. A-D, *G. Cladophlebis australis* (Morrison) Seward, 1904. A, pinna showing details of venation, UQF79731, x 1.5. B, Two fertile pinnae attached to thick rachis, UQF79690, x 2. C, sterile pinna with entire-margined pinnules, UQF79691, x 1.5. D, fertile pinna with flexed pinnules, UQF79704, x 2. E, portion of fertile pinna, UQF79686, x 4. E,F, *Cladophlebis* sp. A, showing pinnules with lobed margins, UQF79679, E x 1, F (counterpart) x 2. H, *Sphenopteris* sp., UQF79699, x 1.5.

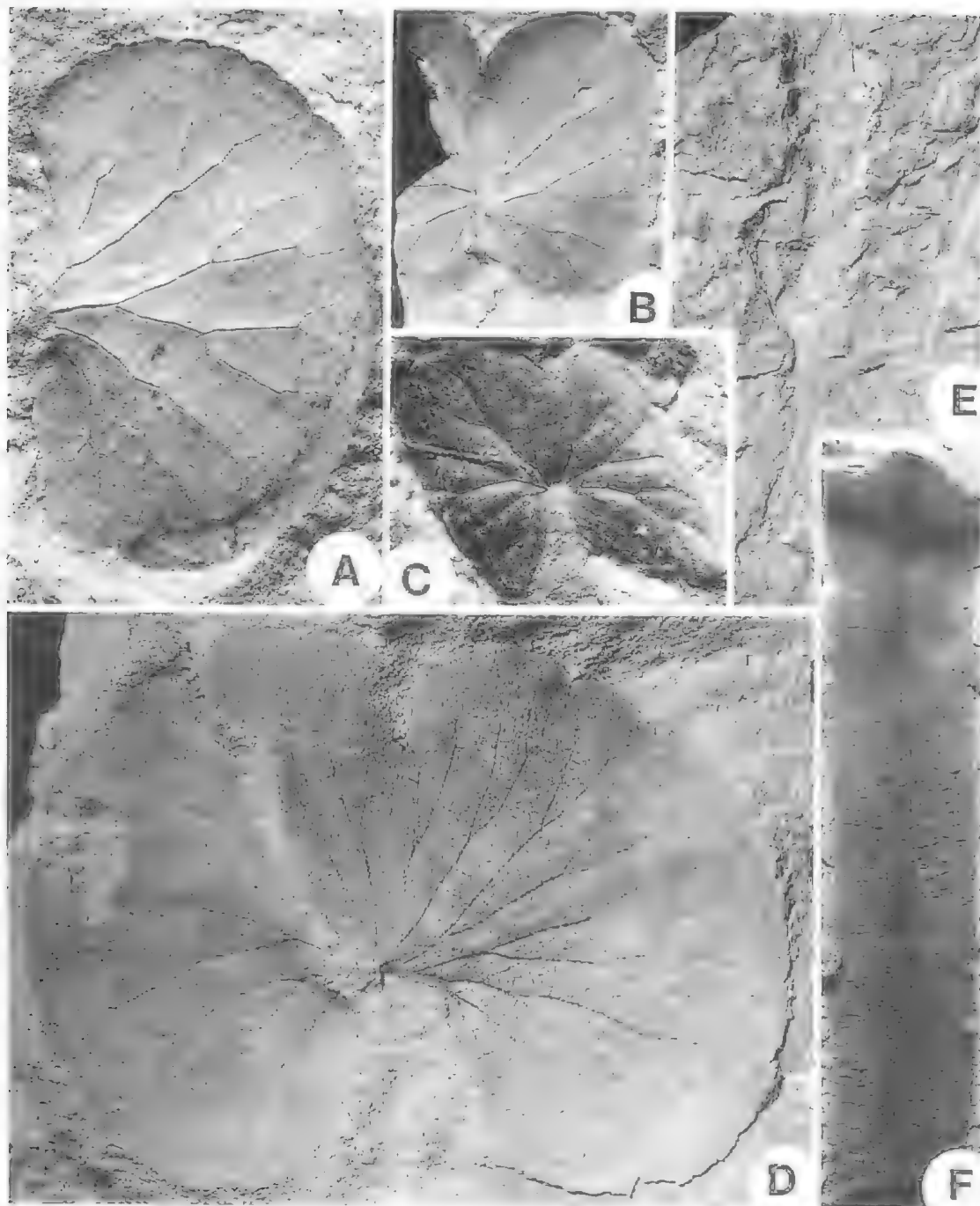


FIG. 4. A-D, *Hausmannia* sp. cf. *H. deferrariisii* Feruglio, 1937. A, half frond showing venation details, UQF79672, x 2. B, UQF79673, x 1. C, UQF79674, x 1. D, large reniform frond, UQF79687, x 1. E, F, *Taeniopteris* sp. cf. *T. spatulata* McClelland, 1850. E, matted examples of very slender leaves, UQF79707, x 1. F, broad leaf showing venation details, UQF79721, x 2.

INCERTAE SEDIS

Sphenopteris (Brongniart) Sternberg, 1825
Sphenopteris sp.
 (Fig. 3H)

MATERIAL EXAMINED
 UQF79699.

DESCRIPTION

Frond at least bipinnate, rachis impression with central ridge flanked by thin (<0.5mm) marginal flanges. Pinnae incomplete (>20mm long, 9mm wide), catadromous, opposite to subopposite, probably ovate to elliptical. Pinnae rachilla depart rachis at 55°–70°. Pinnules ovate to elliptical, alternate, decurrent, reaching 9mm long, 3mm wide, dissected <20% into rounded distal lobes each with an ultimate vein (Fig. 3H). Midvein sinuous, undergoing unequal dichotomies 3–4 times along pinnule. Pinnule midrib departs rachilla at 20°–40°. Fructification and cuticular details unavailable.

COMPARISON AND REMARKS

The single available specimen (Fig. 3H) is referable to *Sphenopteris* because of its bipinnate frond and dissected pinnules with sinuous veins. However, the scant remains prohibit confident specific identification. Fronds attributed to *Coniopteris delicatulata* (Shirley) Walkom 1917, *Coniopteris hymenophylloides* var *australica* Seward (Walkom, 1919), *Coniopteris hymenophylloides* Brongniart (Walkom, 1921) and *Coniopteris* sp. (Hill et al., 1966) probably from the basal Jurassic Landsborough Sandstone of the Nambour Basin, the Purlawaugh Formation of central New South Wales, and the Woodenbong Beds (or Grafton Formation) and the Walloon Coal Measures of the Clarence-Moreton Basin, are possibly conspecific with the Mutdapilly specimen. However, the absence of fertile material does not permit definite assignment to *Coniopteris*. Other Mesozoic Australian sphenopteroid fronds [e.g., *S. lacunosa* Shirley 1898, *S. warragulensis* McCoy 1892, *S. flabellifolia* (Tenison-Woods) Walkom 1919] differ by their less dissected or more elongate pinnules. *Sphenopteris travisii* Stirling 1900 has similar dissected pinnules but these are not so attenuated at the base as those of the Mutdapilly specimen.

INCERTAE SEDIS
 Order PENTOXYLALES
 Family PENTOXYLACEAE

Taeniopteris Brongniart, 1828
Taeniopteris sp. cf. *T. spatulata*
 McClelland, 1850
 (Figs. 4E,F, 5A,B)

MATERIAL EXAMINED
 UQF79707–UQF79710, UQF79715–UQF79721,
 UQF79724, UQF79726.

DESCRIPTION

Leaves highly variable in size and shape, spatulate (Figs 4F; 5A,B) to linear (Fig. 4E), reaching 124mm long, 13mm wide, lamina entire, arrangement on stem uncertain. Lamina very gently tapering towards base, apex rounded acute. Midrib stout, reaching 2mm wide at base, tapering gently towards apex, persistent, longitudinally striate. Secondary veins depart midrib at 80°–90°, typically bifurcating immediately on leaving the midrib then passing straight to margin or bifurcating once more in outer lamina (Figs 4F; 5B). Vein concentration 25–36 per cm at margin. Cuticular details and fructifications unavailable.

COMPARISON AND REMARKS

Taeniopteris leaves from Triassic to mid-Cretaceous Australian deposits show a strong degree of morphological conservatism, differing only slightly in their average sizes and the angle of secondary vein departure from the midrib. Features such as the shape of the leaf apex and the entirety of the lamina margin are variable within populations (Drinnan & Chambers, 1985) and are probably not useful taxonomic features. Cuticular details and the morphology of associated fructifications may be important characters for the specific segregation of *Taeniopteris*-bearing plants but these features are commonly not available. *Taeniopteris* and *Nipaniophyllum* leaves have consistently been found in association with *Carnoconites* (ovulate) and *Sahnia* (pollenate) fructifications from various Gondwanan provinces (Sahni, 1948; Vishnu-Mittre, 1953; Drinnan & Chambers, 1985, 1986) and most are likely to belong to pentoxylalean gymnosperms.

Taeniopteris leaves from the Walloon Coal Measures have traditionally been referred to *T. spatulata* (e.g., Walkom, 1917; Hill et al., 1966; Gould, 1980), a species established for Jurassic to Early Cretaceous Indian material. Queensland and Indian leaves are morphologically very sim-



FIG. 5. A,B, *Taeniopteris* sp. cf. *T. spatulata* McClelland, 1850. A, matted examples of relatively broad *Taeniopteris* leaves, UQF79718 (right), UQF79719 (centre), UQF79720 (far left), x 1. B, UQF79715, x 2. C,D, cf. *Elatocladus confertus* (Oldham & Morris) Halle, 1913. C, several slender, rarely branched, twigs with spirally inserted uni-veined leaves, UQF79696, x 1. D, enlargement of one axis in Fig. 5C, x 3. E,F: indeterminate parallel-veined foliage. E, UQF79714, x 2. F, UQF79735, x 1.5.

ilar, but the Walloon specimens lack critical cuticular data, anatomical details, and fructifications that now appear to be essential for accurate specific determinations within this genus. Most Australian Triassic *Taeniopteris* leaves (e.g., *T. carruthersi* Tenison-Woods 1883, *T. lenticuliforme* (Etheridge) Walkom 1917, *T. dunstani* Walkom 1917) differ from *T. sp. cf. T. spatulata* by their proportionately broader laminae and lesser vein density.

Taeniopteris leaves from Mutdapilly range from relatively broad spatulate forms (Figs 4F; 5A,B) to linear, needle-like examples (Fig. 4E). Although individual leaves can appear quite different, a morphological continuum exists within the population. A similar morphological range is evident in *Taeniopteris* leaves from the Clent Hills Group (Middle Jurassic), Waikawa, New Zealand. *Taeniopteris daintreei* McCoy 1860 and *T. howardensis* Walkom 1919, from the Victorian and Queensland Early Cretaceous respec-

tively, also show close morphological similarities to *T. sp. cf. T. spatulata* but as Drinnan & Chambers (1985) implied, the relationships between the middle and late Mesozoic pentoxylaleans will only be clarified with the discovery of associated fructifications.

INCERTAE ORDINUS

***Elatocladus* Halle emend. Harris, 1979**
cf. *Elatocladus confertus*
 (Oldham & Morris) Halle, 1913
 (Fig. 5C, D)

MATERIAL EXAMINED
 UQF79696.

DESCRIPTION

Slender axes (>30mm long, <2mm wide), some showing irregular branching, bearing numerous widely spaced spirally arranged linear to oblong leaves (Fig. 5C,D). Leaf scars transversely elliptical, reniform, or slit-like. Leaves reaching 8mm long, 0.8mm wide, flattened, univined, margin entire, apex rounded, lower part of leaf gently tapering but base slightly expanded, clasping? or slightly decurrent. Leaves arched basally to depart stem typically at 40°-80°. Attached fructification and cuticular details unavailable.

COMPARISON AND REMARKS

The few available slender axes show narrow flattened univined leaves typical of *Elatocladus* or *Rissikia* species. Leaves and leaf scars on the axes (Fig. 5D) indicate spiral leaf insertion but, owing to indifferent preservation, it is unclear whether the leaves were naturally twisted to lie in a single plane or whether the distichous arrangement is due to compression. These leaves are significantly smaller than those traditionally attributed to *Elatocladus plana* (Feistmantel) Halle and lack the contracted lamina base typical of that species. Although the leaves are slightly more sparse than previously figured examples, the Mutdapilly fossils are closest to *Elatocladus confertus* (Oldham & Morris) Halle 1913. Sterile *Elatocladus* remains have traditionally been regarded as coniferous and have sometimes been compared to the Podocarpaceae. However, *Elatocladus*-type remains have previously been found associated with *Palissya* (Edwards, 1934) and sometimes assigned to that genus (Shirley, 1902) although a physical connection between sterile foliage and fertile cones has not been dem-

onstrated. As the structure of *Palissya* is atypical for conifers we suggest their placement together with *Elatocladus* under open nomenclature until their phylogenetic affinities are more clearly resolved. The common association of *Elatocladus* foliage with *Palissya* cones in Australian and New Zealand Jurassic and Cretaceous deposits supports an affinity between these fossils. However, other plant remains (notably *Taeniopteris* species) are also co-preserved with these fossils and are possible candidates for foliage associated with *Palissya*.

INCERTAE ORDINUS Family PALISSYACEAE

***Palissya* Endlicher, 1847**
***Palissya ovalis* Parris,**
 Drinnan & Cantrill, 1995
 (Fig. 6A-I)

MATERIAL EXAMINED

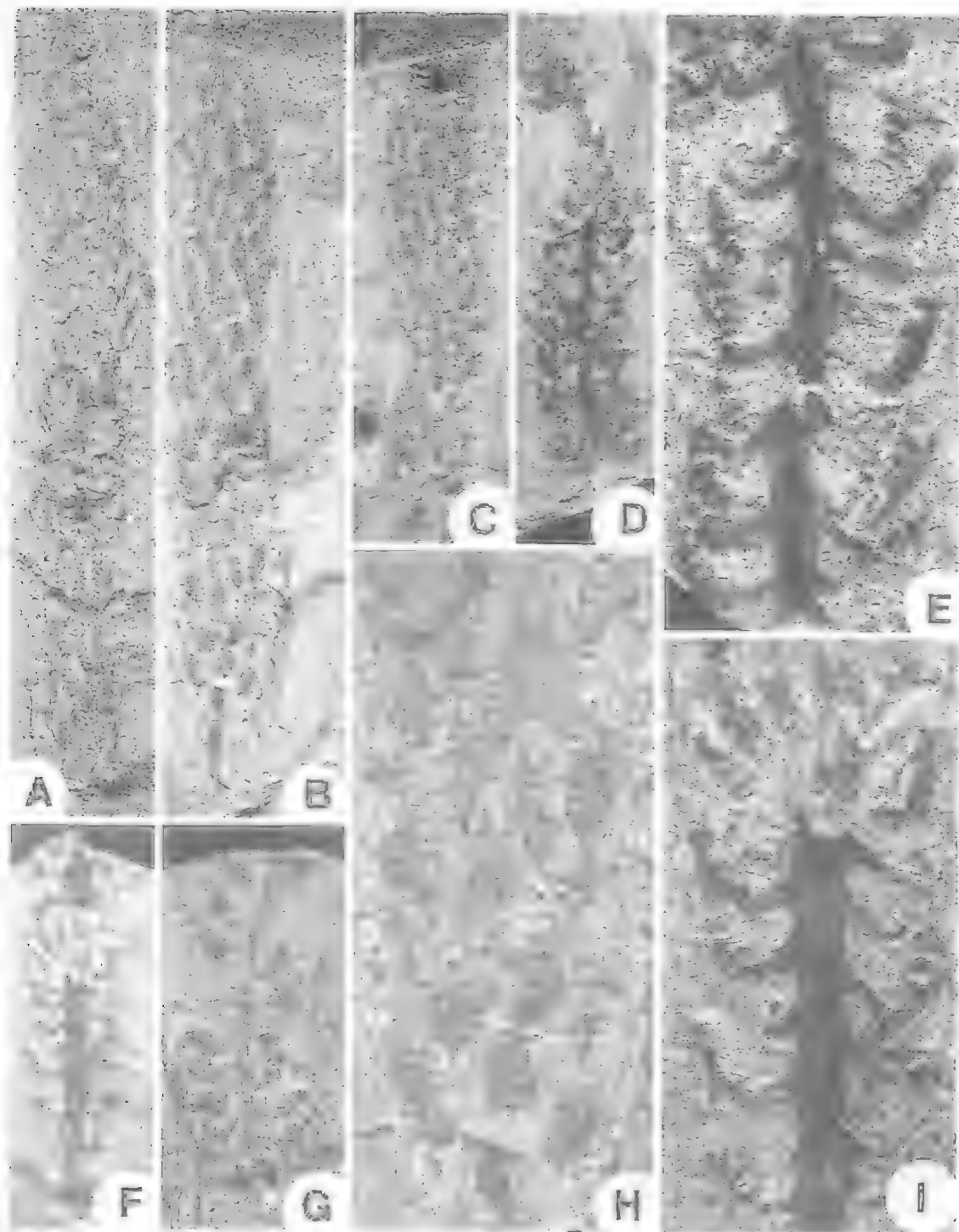
UQF79671, UQF79678, UQF79682, UQF79685, UQF79695, UQF79697, UQF79698, UQF79701-UQF79703, UQF79722, UQF79727.

DESCRIPTION

Elongate cone greater than 120mm long, 14mm wide, consisting of a central axis up to 2.5mm wide, bearing helically arranged sporophylls. Sporophylls stalked, oval, lamina up to 5mm long and 2.5mm wide, stalk 4mm long. Sporophylls bear 7 or 8 pairs of adaxial processes.

COMPARISON AND REMARKS

None of the cones are complete, but several seem to be missing only a relatively small proximal portion. Some specimens are cleaved longitudinally through the cone (Fig. 6D-G,I), revealing the axis and sporophylls in longitudinal section. In others, the part and counterpart have separated close to the surface of the cone, revealing details of the cone in surface view (Fig. 6A-C, H). Cones are preserved in both closed and open states. In closed cones the sporophylls are tightly overlapping and closely appressed to the cone axis (Fig. 6A-C). In most of these specimens, cleavage of the part and counterpart has occurred around the surface of the cone through the sporophyll blade, revealing a prominent dendroid pattern on the abaxial surface of the sporophylls (Fig. 6H). This pattern results from pairs of overlapping adaxial cup-shaped processes that remain embedded in the part when the sporophyll blade separates with the counterpart (Parris et al., 1995). In open cones, the sporophylls have re-



flexed away from the axis and the sporophylls and their adaxial processes are often visible in lateral view (Figs 6D-G,I). These processes were interpreted by Parris et al. (1995) as probably associated with ovules or seeds, but there was no conclusive evidence of any attached sporangiate structures in any of the species of *Palissya* that they examined, nor are they apparent on the Mutdapilly cones discussed here.

These cones are very similar to *Palissya ovalis* described by Parris et al. (1995) from several other southeast Queensland localities in the Walloon Coal Measures. The few specimens of *P. ovalis* previously available show only five or six pairs of adaxial processes per sporophyll, whereas specimens from Mutdapilly, which are more numerous and complete, have seven or eight pairs of processes per sporophyll (Fig. 6H). However, this may reflect that the small sample of the original *P. ovalis* material was too fragmentary to reveal accurately the sporophyll detail. There are also some minor differences in sporophyll size, but these alone are not sufficient to warrant status as a separate species. *Palissya bartrami* Edwards 1934 from the Middle Jurassic of New Zealand is similar in size and gross morphology, but the specimens examined by Parris et al. (1995) appeared to have only three or four pairs of sporophylls. Because of the similarity of the Mutdapilly cones to *P. ovalis* from elsewhere in the Walloon Coal Measures, we have assigned the Mutdapilly cones to that species. Future accumulation of specimens from Australia and New Zealand will almost certainly necessitate a revision of the taxonomy of *Palissya*.

INCERTAE SEDIS

Parallel-veined foliage/axes (Fig. 5E, F)

MATERIAL EXAMINED

UQF79711-UQF79714, UQF79725, UQF79734, UQF79735.

DESCRIPTION

Linear leaves/axes reaching at least 80mm long, 5mm wide, margin entire, apex rounded,

base unavailable, arrangement on axis unknown. Venation parallel, dichotomous?, vein concentration 4-9 per 2mm measured transverse to venation. Indistinct linear striations common on lamina between veins. Lamina sometimes split longitudinally between the veins.

COMPARISON AND REMARKS

All specimens are fragmentary. Some undoubtedly represent leaves or detached pinnules with rounded apices (Fig. 5E) whereas others (Fig. 5F) may constitute portions of longitudinally striate rachises or axes. Several specimens show longitudinal splitting of the lamina/axis between the veins. The specimens are reminiscent of detached cycadalean or bennettitalean pinnules but none can be identified with certainty. However, the absence of other recognizable pinnate cycadophytic foliage in this assemblage is notable given its frequent occurrence elsewhere in the Walloon Coal Measures and lateral equivalents (Gould, 1974, 1980) and in Middle Jurassic strata of other parts of the world.

DISCUSSION OF THE FLORA

The abundant, relatively complete remains of ferns and equisetaleans preserved within fine-grained sediments accords with the low-energy paludal/lacustrine depositional environments suggested for parts of the Walloon Coal Measures by Exon et al. (1974) and Cranfield et al. (1976). *Taeniopteris* leaves are also well-represented on several bedding planes. While Gould (1974, 1975, 1980) noted that remains of pteridophytes and pentoxyleans were locally abundant (especially near the base of coal seams) he indicated that the flora of the coal measures as a whole was dominated by araucarian and podocarp conifers. The notable absence of pinnate cycadophyte fronds and pachypterid seed ferns so common to other Australian Jurassic assemblages may indicate deposition away from better drained sites (where those plants may have been more abundant). Nevertheless, common *Palissya* cones and scarce *Elatocladus*-like foliage together with isolated parallel-veined leaflets constitute minor though significant conifer and possible pterido-

FIG. 6. A-I, *Palissya ovalis* Parris, Drinnan & Cantrill, 1995. A, cone exposed by fracturing through the sporophyll blades, UQF79673, x 1. B-H, near-complete cone with up to eight pairs of overlapping cup-shaped processes on each sporophyll exposed by cleavage through the sporophyll blades, UQF79695, B x 1, H x 3. C, UQF79701, x 1. D-E, cones exposed by cleavage along axis, showing recurved sporophylls and adaxial cup-like processes, D, UQF79722, x 1, E, UQF79685, x 3. F-I, axially cleft, open cone, showing details of recurved sporophylls, UQF79671, F x 1, I x 3. G, open cone, UQF79702, x 1.

sperm components of the flora. Ginkgophytes are notably absent from the Mutdapilly collections. This absence was also recognized from other Walloon Coal Measure assemblages investigated by Gould (1974, 1980) and is surprising given that group's abundance and virtually cosmopolitan distribution in the Jurassic.

The preserved foliage yields little definitive information concerning the palaeoclimate during deposition of the Walloon Coal Measures. *Taeniopteris* leaves in the assemblage frequently occur as complete leaves in matted layers (Figs 4E, 5A) consistent with their interpretation as the foliage of deciduous pentoxylaleans (Drinnan & Chambers, 1985, 1986). The probable deciduous character of these plants together with distinct growth banding evident in pentoxylalean and conifer woods elsewhere in the Walloon Coal Measures (Gould, 1980) suggests some climatic seasonality but whether the plants were responding to variation in rainfall, temperature, photoperiod or some other environmental factor is indeterminable. Modern dipteridacean ferns occur only in subtropical to tropical humid environments (Corsin & Waterlot, 1979). It is possible that extinct representatives of this family such as *Hausmannia* sp. cf. *H. defarrariisii* were also restricted to humid megathermal-mesothermal habitats although the latitude of the Moreton Basin during the Jurassic was probably around 60° (Embleton, 1984) or as high as 65°-75° (Smith et al., 1973).

Floristic similarities are evident at the generic level between the Middle Jurassic Mutdapilly assemblage and Australian Early Jurassic and Late Jurassic to Early Cretaceous floras, but differences are generally evident at species level. Notable differences are the appearance of *Hausmannia* ferns, the scarcity of phlebopterid ferns, and the apparent absence of *Sagenopteris* in the Walloon flora compared to Early Jurassic assemblages (Walkom, 1917; Jones & de Jersey, 1947; Gould, 1974, 1975, 1980). Late Jurassic floras are poorly known from the Australian region although Day (1964) recorded an assemblage from the Surat Basin's Orallo Formation that is similar to the Walloon Coal Measures apart from the presence of ginkgoaleans. Early Cretaceous floras commonly differ either by the occurrence of more abundant bennettitalean remains or by the presence of ginkgoaleans, phyllopteroid ferns, and herbaceous isoëtalean lycophytes (Walkom, 1928, 1944; Glaessner & Rao, 1955; Douglas, 1969; Gould, 1978; Drinnan & Chambers, 1986).

A strikingly similar flora to the Mutdapilly assemblage was described by Edwards (1934) from the Clent Hills Group, Waikawa, New Zealand. The New Zealand assemblage, regarded as Middle Jurassic (Bajocian-Bathonian) by Arber (1917), Edwards (1934), and Suggate et al. (1978), yields similar equisetalean axes, sphenopterid remains, cladophlebid fronds, taeniopterid leaves, *Palissya* cones, and *Elatocladus*-type foliage to the Mutdapilly flora. The Waikawa assemblage differs by the presence of lycophyte axes, pinnate Bennettitalean fronds, and *Araucarian* remains and by the absence of dipteridacean ferns.

The Hope and Botany Bay floras of the Antarctic Peninsula long considered to be Late Jurassic or Early Cretaceous in age have recently been regarded as Early Jurassic or older (Rees, 1993). These Antarctic Peninsula floras contain similar, but mostly not identical, forms of *Equisetum*, *Cladophlebis*, *Sphenopteris*, *Hausmannia*, *Otozamites*, *Elatocladus* and *Pagiophyllum* species to the Walloon assemblages and differ in also yielding *Sagenopteris*, *Pseudoceras*, and *Goeppertella* and by lacking *Taeniopteris* (Gee, 1989; Rees, 1993). The occurrence of *Sagenopteris* and *Goeppertella* foliage in the Hope/Botany Bay assemblages reflects closer similarities to the flora of the Early Jurassic Marburg Formation of the Clarence-Moreton Basin (Gould, 1971).

CONCLUSIONS

The Mutdapilly plant fossil assemblage is rich in pteridophytes (most notably *Cladophlebis australis* and *Hausmannia* sp. cf. *H. defarrariisii*) and probable pentoxylaleans (*Taeniopteris* sp. cf. *T. spatulata*). *Palissya* cones are also abundantly represented in the assemblage. The flora differs from typical Walloon Coal Measure suites by a deficiency in bennettitalean and conifer (especially *Araucaria*, *Allocladus*, and *Pagiophyllum*) species. The Mutdapilly assemblage is most similar to those described by Gould (1980) from the base of coal seams elsewhere in the Walloon Coal Measures and perhaps reflects a specialized pioneer mire community. In other respects the assemblage has elements in common with a number of Middle Jurassic Gondwanan floras, reaffirming the age assigned to the Walloon Coal Measures by previous palynological and stratigraphic studies. The flora provides little definitive palaeoclimatic information but a moist seasonal climatic regime is envisaged based on the categories

of plants preserved, the apparent deciduous character of *Taeniopteris* leaves, and prominent growth rings evident in permineralized wood elsewhere in the Walloon Coal Measures.

ACKNOWLEDGEMENTS

Andrew Simpson and Dr John Jell of the Department of Earth Sciences, The University of Queensland are thanked for arranging the loan of the specimens.

LITERATURE CITED

- ANDERSON, J.M. & ANDERSON, H.M. 1983. 'Palaeoflora of Southern Africa, Molteno Formation (Triassic), Volume 1 (Part 1. Introduction; Part 2. Dicrodium)'. (A.A. Balkema, Rotterdam).
- ARBER, E.A.N. 1917. The earlier Mesozoic floras of New Zealand. New Zealand Geological Survey Palaeontological Bulletin 6: 1-80.
- BARTHOLOMAI, A. 1966. Fossil footprints in Queensland. Australian Natural History 15: 147-150.
- BOSE, M.N. & SAH, S.C.D. 1968. Some pteridophytic remains from the Rajmahal Hills, Bihar. Palaeobotanist 16: 12-28.
- CANTRILL, D.J. & WEBB, J.A. 1987. A reappraisal of *Phyllopteroides* Medwell (Osmundaceae) and its stratigraphic significance in the Lower Cretaceous of eastern Australia. Alcheringa 11: 59-85.
- CORSIN, P. & WATERLOT, M. 1979. Paleobiogeography of the Dipteridaceae and Matoniaceae of the Mesozoic. IV International Gondwana Symposium Vol. 1. 51-70. (Geological Survey of India. Hindustan Publishing Corporation, Delhi).
- CRANFIELD, L.C., SCHWARZBOCK, H. & DAY, R.W. 1976. Geology of the Ipswich and Brisbane 1:250 000 Sheet areas. Geological Survey of Queensland Report 95: 1-176.
- DAY, R.W. 1964. Stratigraphy of the Roma-Wallumbilla area. Geological Survey of Queensland Publication 318: 1-23.
- DE JERSEY, N.J. 1960. Jurassic spores and pollen grains from the Rosewood Coalfield. Geological Survey of Queensland Publication 294: 1-14.
- DE JERSEY, N.J. & PATEN, R.J. 1964. Jurassic spores and pollen grains from the Surat Basin. Geological Survey of Queensland Publication 322: 1-18.
- DOUGLAS, J.G. 1969. The Mesozoic floras of Victoria. Parts 1 and 2. Geological Survey of Victoria Memoir 28: 1-310.
- DRINNAN, A.N. & CHAMBERS, T.C. 1985. A reassessment of *Taeniopteris daintreei* from the Victorian Early Cretaceous: a member of the Pentoxylales and a significant Gondwanaland plant. Australian Journal of Botany 33: 89-100.
1986. Flora of the Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), south Gippsland, Victoria. Association of Australasian Palaeontologists Memoir 3: 1-77.
- EDWARDS, W.N. 1934. Jurassic plants from New Zealand. Annals and Magazine of Natural History, Series 10, 13: 81-109.
- EMBLETON, B.J.J. 1984. Past global settings. Continental palaeomagnetism. Pp. 11-16. In: Veevers, J.J. (ed.) 'Phanerozoic Earth History of Australia'. Oxford Monographs on Geology and Geophysics no. 2. (Oxford Science Publications: Oxford).
- EXON, N.F., REISER, R.F., CASEY, D.J. & BRUNKER, R.L. 1974. The post-Palaeozoic rocks of the Warwick 1:250 000 Sheet area, Queensland and New South Wales. Australian Bureau of Mineral Resources, Geology and Geophysics, Report 140: 1-70.
- FIELDING, C.F. 1993. The Middle Jurassic Walloon Coal Measures in the type area, the Rosewood-Walloon Coalfield, SE Queensland. Australian Coal Geology 9: 4-15.
- GEE, C.T. 1989. Revision of the Late Jurassic/Early Cretaceous flora from Hope Bay, Antarctica. Palaeontographica 213B: 149-214.
- GLAESSNER, M.F. & RAO, V.R. 1955. Lower Cretaceous plant remains from the vicinity of Mount Babbage, South Australia. Transactions of the Royal Society of South Australia 78: 134-140.
- GOULD, R.E. 1968. Morphology of *Equisetum laterale* Phillips, 1829, and *E. bryanii* sp. nov. from the Mesozoic of south-eastern Queensland. Australian Journal of Botany 16: 153-176.
1971. Report on plant fossils from Durikai, south-eastern Queensland. Appendix 3. Pp. 63-64. In: Exon, N.F., Reiser, R.F., Casey, D.J. & Brunker, R.L. 'The post-Palaeozoic rocks of the Warwick 1:250 000 Sheet area, Queensland and New South Wales', Australian Bureau of Mineral Resources, Geology and Geophysics, Report 140.
1973. A new species of *Osmundacaulis* from the Jurassic of Queensland. Proceedings of the Linnean Society of New South Wales 98: 86-94.
1974. The fossil flora of the Walloon Coal Measures: a survey. Proceedings of the Royal Society of Queensland 85: 33-41.
1975. The succession of Australian pre-Tertiary megafossil floras. Botanical Review 41: 453-483.
1978. Report on plant fossils from the Tarlton Range, Tobermory 1: 250 000 Sheet area, Northern Territory. Pp. 87-88. In: Senior, B.R., Mond, A. & Harrison, P.L. 'Geology of the Eromanga Basin'. Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin 167.
1980. The coal-forming flora of the Walloon Coal Measures. Australian Coal Geology 1: 83-105.
- HALLE, T.G. 1913. The Mesozoic flora of Graham Land. Wissenschaftliche Ergebnisse der Schwedischen Südpolar-expedition 1901-1903 3: 1-123.

- HARRIS, T.M. 1961. 'The Yorkshire Jurassic Flora. 1. Thallophyta-Pteridophyta'. (British Museum of Natural History: London).
- HERBST, R. 1960. Descripción de ejemplares fértiles de «*Hausmannia (Protorhipis) papilio*» Feruglio, procedentes de los estratos de Baqueró (Santa Cruz). *Acta Geologica Lilloana* 3: 227-232.
1971. Revision de las especies Argentinas del género *Cladophlebis*. *Ameghiniana* 8: 265-281.
1979. Review of the Australian Dipteridaceae. *Proceedings of the Linnean Society of New South Wales* 103: 7-21.
- HILL, D., PLAYFORD, G. & WOODS, J.T. 1966. 'Jurassic fossils of Queensland'. (Queensland Palaeontographical Society: Brisbane).
- JONES, O.A. & DE JERSEY, N.J. 1947. The flora of the Ipswich Coal Measures. Morphology and floral succession. *Papers of the Department of Geology, University of Queensland (N.S.)* 3: 1-88.
- LONGOBUCCO, M.I., AZCUY, C.L. & AGUIRRE URRETA, B. 1985. Plantas de la Formación Kachaike, Cretácico de la Provincia de Santa Cruz. *Ameghiniana* 21: 305-315.
- MOLNAR, R.E. 1991. Fossil reptiles in Australia. Pp. 605-702. In Vickers-Rich, P., Monaghan, J.M., Baird, R.F. & Rich, T.H. 'Vertebrate Palaeontology of Australasia'. (Pioneer Design Studios: Melbourne).
- PARRIS, K.M., DRINNAN, A.N. & CANTRILL, D.J. 1995. *Palissya* cones from the Mesozoic of Australia and New Zealand. *Alcheringa* 19: 87-111.
- REES, P.McA. 1993. Dipterid ferns from the Mesozoic of Antarctica and New Zealand and their stratigraphical significance. *Palaeontology* 36: 637-656.
- RIGBY, J.F. 1978. Jurassic plant fossils from the Walloon Coal Measures at Rosewood Consolidated Colliery. *Queensland Government Mining Journal* 78: 320-325.
- SAHNI, B. 1948. The Pentoxyleae: a new group of Jurassic gymnosperms from the Rajmahal Hills of India. *Botanical Gazette* 110: 47-80.
- SHIRLEY, J. 1902. Fossil plants from Duaringa, Ipswich, Dawson River, and Stanwell and on fossil woods from the Ipswich Beds, Boggo Road, Brisbane. *Geological Survey of Queensland Publication* 171: 1-28.
- SMITH, A.G., BRIDEN, J.C. & DREWRY, G.E. 1973. Phanerozoic world maps. *Special Papers in Palaeontology* 12: 1-42.
- SUGGATE, R.P., STEVENS, G.R. & TEPUNGA, M.T. 1978. 'The Geology of New Zealand'. (New Zealand Geological Survey; Government Printer: Wellington).
- TURNER, S. & ROZEFELDS, A., 1987. First Jurassic actinopterygian fish from Queensland. *Memoirs of the Queensland Museum* 25 (1): 201-206.
- VISHNU-MITRE. 1953. A male flower of the Pentoxyleae with remarks on the structure of the female cones of the group. *Palaeobotanist* 2: 75-84.
- WALKOM, A.B. 1917. Mesozoic floras of Queensland. Part 1.-continued. The flora of the Ipswich and Walloon Series. (c) Filicales, etc. *Geological Survey of Queensland Publication* 257: 1-65.
1919. On a collection of Jurassic plants from Bexhill, near Lismore, N.S.W. *Proceedings of the Linnean Society of New South Wales* 44: 180-190.
1921. Mesozoic floras of New South Wales. Part 1.-Fossil plants from Cockabutta Mountain and Talbragar. *Memoirs of the Geological Survey of New South Wales, Palaeontology* 12: 1-21.
1928. Fossil plants from Plutoville, Cape York Peninsula. *Proceedings of the Linnean Society of New South Wales* 53: 145-150.
1944. Fossil plants from Gingin, W.A. *Journal of the Royal Society of Western Australia* 28: 201-207.
- WHITE, M.E. 1961a. Plant fossils from the Canning Basin, Western Australia. Pp. 291-320. In Veevers, J.J. & Wells, A.T. 'The Geology of the Canning Basin, Western Australia'. Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin 60.
- 1961b. Report on 1960 collections of Mesozoic plant fossils from the Northern Territory. Australian Bureau of Mineral Resources, Geology and Geophysics, Record 1961/146: 1-26. (unpublished).
1966. Report on 1965 plant fossil collections. Australian Bureau of Mineral Resources, Geology and Geophysics, Record 1966/111: 1-10. (unpublished).

A CENOMANIAN FLORA FROM THE WINTON FORMATION, EROMANGA BASIN, QUEENSLAND, AUSTRALIA

STEPHEN McLOUGHLIN, ANDREW N. DRINNAN AND ANDREW C. ROZEFELDS

McLoughlin, S., Drinnan, A. N. & Rozefelds, A. C. 1995 06 01: A Cenomanian Flora from the Winton Formation, Eromanga Basin, Queensland, Australia. *Memoirs of the Queensland Museum* 38(1): 273-313. ISSN 0079-8835.

A middle Cretaceous (Cenomanian) fossil flora from the Winton Formation of central Queensland consists of six taxa of ferns, four conifers, one ginkgophyte, one pentoxylalean, and eight angiosperm leaf types. It is the oldest impression flora to contain abundant angiosperm leaves to date described in detail from Australia, and provides the first, direct, macrofossil evidence of the transition from gymnosperm- to angiosperm-dominated floras in Australia during the Cretaceous. The angiosperm leaves are mostly hamate types of probable fagaceous or betulaceous affinity, but precise relationships are unclear. The Winton angiosperm assemblages show some similarity to Late Cretaceous floras of New Zealand.

□ Late Cretaceous, Cenomanian, Winton Formation, Eromanga Basin, palaeobotany, angiosperms, pteridophytes, conifers, ginkgophytes.

Stephen McLoughlin, Andrew N. Drinnan, Andrew C. Rozefelds, School of Botany, University of Melbourne, Parkville, Victoria 3052, Australia; 10 January 1995.

Lack of Australian Late Cretaceous macrofossil floras has long hindered understanding of the origins, diversification, and biogeography of early austral angiosperms and conifers. Earliest records of angiosperms in the Australian fossil record are rare occurrences of dispersed monosulcate pollen grains from the Barremian of the Eromanga Basin, southern Queensland (Burger, 1988) and the Barremian-Aptian or early Albian Koonwarra Fossil Bed, southeastern Victoria (Dettmann, 1986). It is not until the mid-Albian that the monosulcate pollen types become significant components of Australian palynofloras either in terms of diversity or abundance; triaperturate pollen is first recorded in the middle Albian (Burger, 1988). The palynology and biostratigraphy of Australian Cretaceous strata are well documented (Dettmann & Playford, 1969; Burger, 1973, 1980, 1988; Stover & Evans, 1973; Playford et al., 1975; Morgan, 1980). Particular emphasis has been placed on the early angiosperm component of Australian Cretaceous pollen floras (e.g., Dettmann, 1973; Dettmann et al., 1992; Burger, 1990, 1993), and a progressive increase in the diversity of angiosperms beginning at about the Aptian and continuing through the Late Cretaceous is well documented. Although the systematic affinities of the suite of pollen taxa that account for this initial diversity are mostly unknown, they are morphologically similar to the pollen found in contemporaneous sediments elsewhere in the world and have been ascribed to the same form-genera and often species. Toward the end of the

Cretaceous the unique Gondwanan component of the extant Australian angiosperm flora is recognizable (*Nothofagus*, Proteaceae, Winteraceae, Epacridaceae). A similar palynostratigraphic sequence occurs in New Zealand (Couper, 1953, 1960; Raine, 1984) and Antarctica (Dettmann & Thomson, 1987; Dettmann 1989).

Owing to the paucity of outcropping Late Cretaceous sediments in Australia, reports of Australian Cretaceous angiosperm leaf remains are far less numerous and informative. Medwell (1954b) and Douglas (1969) discussed several unidentified angiosperm leaf and cuticle types from the latest Early Cretaceous of western Victoria, and Taylor & Hickey (1990) reported on a small, magnoliid, angiospermous leaf from the Koonwarra Fossil Bed. Walkom (1919a) described and illustrated several leaves from the Albian Burrum and Styx Coal Measures of central Queensland. As a consequence, there is no comprehensive body of macrofossil evidence relating to the mid-Cretaceous diversification of angiosperms in Australia, the early development of the modern Australian flora, or the non-angiosperm floristic element that accompanied the change from gymnosperm-dominated Early Cretaceous floras to angiosperm-dominated Late Cretaceous and Tertiary floras. The flora described here from the Cenomanian Winton Formation is the first Australian Late Cretaceous leaf megafloora to be recorded in detail.

GEOLOGICAL SETTING

The Winton Formation extends over a broad area of southwestern Queensland, northeastern South Australia and northwestern New South Wales. It consists largely of siltstones and volcanolithic sandstones with minor mudstones and coals (Senior et al., 1978), reaching thicknesses of around 1200m in central parts of the basin (Moore & Pitt, 1984). The formation is the uppermost unit of the Manuka Subgroup within the Rolling Downs Group and incorporates the youngest Cretaceous strata of the Eromanga Basin. Fielding (1992) recognized three major facies associations within the unit, representing major channel, flood basin, and mire environments. Fielding (1992) interpreted the Winton Formation succession as an alluvial plain deposit generated by fluvial systems draining inwardly towards the basin depocentres where more persistent lacustrine conditions may have existed as evidenced by the presence of a range of fossilized dinoflagellate taxa at least in lower parts of the formation (Morgan, 1980).

The Winton Formation conformably overlies shallow marine and coastal deposits of the Mackunda Formation dated as Albian on the basis of invertebrate and palynomorph assemblages (Day et al., 1983). The Winton Formation has yielded spore-pollen assemblages belonging to the *Phimopollenites pannosus* or succeeding *Appendicisporites distocarinatus* zone of probable late Albian to Cenomanian age (Dettmann & Playford, 1969; Burger, 1970; Morgan, 1980; Helby et al., 1987). Moore & Pitt (1984), on the basis of unpublished palynological data suggested that the uppermost beds of this formation in central parts of the basin may have been deposited in the late Cenomanian or early Turonian. The Winton Formation also contains freshwater bivalves, insects, vertebrate body fossils, and dinosaur trackways of limited biostratigraphic utility (Dettmann et al., 1992).

The Winton Formation is disconformably overlain by Late Palaeocene to Eocene fluvial sediments of the Eyre Formation and regionally equivalent units (Day et al., 1983). These strata have been affected by several phases of duricrust development during the Palaeogene and Neogene. Low topographic relief, deep weathering, and duricrust cover commonly make distinction of the Winton Formation from overlying Palaeogene sediments difficult in isolated exposures. The plant assemblages described here probably derive from the Winton Formation

based on lithological criteria and the presence of typical Cretaceous plant groups (phyllopteroid ferns, *Taeniopteris*, and ginkgoaleans). The macrofossil-bearing samples obtained from outcrop are too oxidized for palynological investigation.

MATERIALS AND METHODS

Plant fossils described here come from several outcrop localities in the Winton-Longreach district of central Queensland (Fig. 1). Illustrated specimens are lodged with the Queensland Museum (bearing catalogue numbers prefixed 'QMF') or the National Museum of Victoria (specimens prefixed 'NMVP'). Queensland Museum fossil locality numbers are prefixed 'L'. Some of the material was collected by Queensland Museum staff who endeavoured to obtain representative examples of the range of taxa from each locality. Other material was contributed by local landowners and opal miners for which only generalized locality details are available. Material from the following localities was investigated:

L165 - Western side of Tully Range (Brighton Downs 1:250 000 map), 23°02'S 142°23'E.

L224 - Cork Station (Brighton Downs 1:250 000 map); 23°01'S 142°24'E.

L406 - 6 km northwest of Whyrallah Homestead (Mackunda 1:250 000 map); 22°43'S 142°21'E.

L552 - New Year Creek, southeast of Mayneside, south-southwest of Winton; latitude and longitude uncertain.

L717 - 2 km west of Dalkeith Homestead, south of Winton; 23°31'S 143°11'E.

QMF17458 - Conway's Claim, near Opalton, south of Winton; latitude and longitude uncertain.

Plant fossils are preserved as impressions in buff, pale yellow, dark brown, or pink, siltstones or fine-grained lithic sandstones. Small cross-laminae and parallel laminae are evident in the host rocks and together with the relatively undamaged leaf remains and numerous slender invertebrate (?oligochaete) trails, they suggest relatively low energy, ?lacustrine, depositional environments. Many impressions are coated by a thin film of iron-oxides that occasionally shows indistinct epidermal imprints, but no organic matter is preserved. Cuticular features could not be discerned.

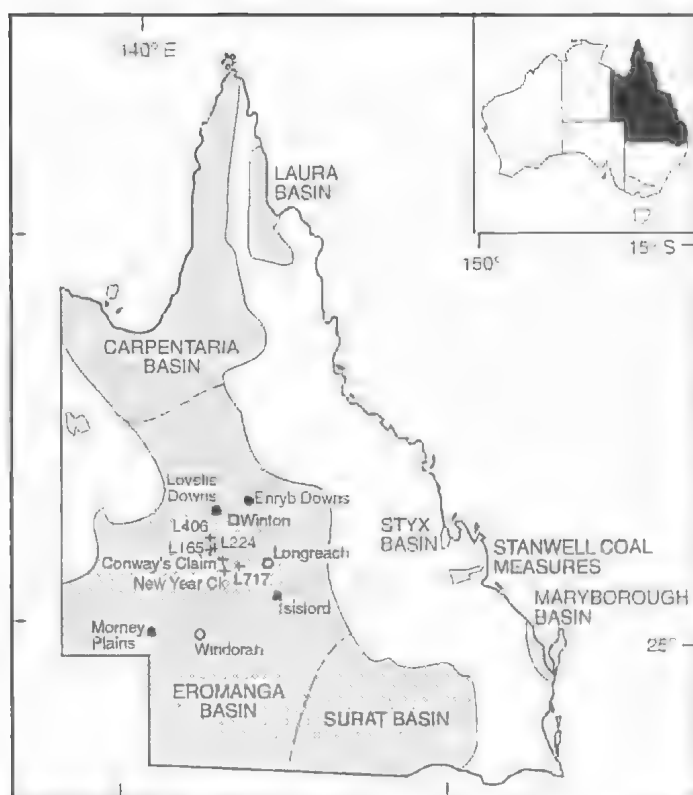


FIG. 1. Map of Queensland showing the distribution of Cretaceous sedimentary basins, selected towns (open circles), fossil localities studied here (crosses), and localities discussed in previous studies (closed circles).

PREVIOUS STUDIES OF WINTON FORMATION PLANT FOSSILS

Bose (1955) described equisetalean nodal diaphragms (*Equisetites* sp.), araucarian foliage-bearing shoots (*Araucaria* cf. *fletcheri* Selling, *Araucaria* sp.), bark impressions, and detached taxodiaceous foliage-bearing twigs and cones (*Athrotaxis australis* and *A. sellingeri* respectively) from Portland Downs Station, 25 km northwest of Isisford, central Queensland (Fig. 1). Bose (1955) proposed an (?) Oligocene age for the assemblage based on limited stratigraphic information. Bose's (1955) assemblage appears to contain several elements in common with the material described below and with that illustrated by Peters & Christophel (1978). More recent geological mapping indicates that the Winton Formation outcrops extensively through the Isisford area (Day et al., 1983) and is likely to be the source of Bose's material.

Whitehouse (1955) indicated the presence of *Protophyllocladus*, *Nathorstia*, and dicotyledonous leaves in the Winton Formation but these determinations were not substantiated by descriptions or illustrations.

White (1966) noted the presence of araucariaceous foliage (which she referred to *Pagiophyllum peregrinum* Lindley & Hutton) from near the base of the Winton Formation at a locality approximately 11.2 km southeast of Enryb Downs Homestead, Winton district (Fig. 1). She also recognized linear, parallel-veined, possible cycadophyte pinnules from the same locality. White's (1966) specimens were not figured. She suggested a Jurassic or Lower Cretaceous age for this material.

White (1974) illustrated a slab of ferruginous sandstone from the Winton Formation, 5 km east of Morney Plains Homestead (west of Windorah; Fig. 1). The slab bears a large angiosperm leaf (which White referred to *Artocarpidium stuartii* Ettingshausen) and linear, striate, plant fragments (assigned to *Podozamites* sp. and *Equisetites* sp.). She also recorded the presence on another slab of a small conifer twig ascribed to *Pagiophyllum peregrinum*, and regarded the assemblage as Late Cretaceous in age.

Peters & Christophel (1978) described permineralized taxodiaceous cones (*Austrosequoia wintonensis*) from Lovelock Downs Station (22°12'00"S 142°31'30"E), approximately 50 km northwest of Winton (Fig. 1). This locality also yields siliceous permineralized remains of various ferns, conifers, and angiosperms (Peters & Christophel, 1978) several of which appear to show surface morphological features identical to species here described from impressions. A range of plant remains from this assemblage was described by Peters (1985). Large collections of Winton Formation permineralized remains held by the Queensland Museum offer the potential for greater insights into the anatomy of plants in these austral early angiosperm floras.

Dettmann et al. (1992) illustrated a branched, foliage-bearing, araucarian twig and a cluster of araucarian cone scales from the Winton Forma-

tion of Whyrallah Station, Winton district, in their review of the Australian Cretaceous biota and terrestrial environments.

SYSTEMATIC PALAEOBOTANY

Phylum PTERIDOPHYTA
Class FILICOPSIDA
Order FILICALES
Family ?OSMUNDACEAE
Phyllopteroides Medwell, 1954

Phyllopteroides macclymontae sp. nov.
(Figs 2A-D, 3A-H)

MATERIAL EXAMINED

HOLOTYPE: L717: QMF32543.

PARATYPES: L717: QMF32503, QMF32514, QMF32520, QMF32527, QMF32533, QMF32544, QMF32545, QMF32567, QMF32574, QMF32594-5, QMF32618, QMF32619, QMF32621, QMF32624, QMF32625, QMF32628-30.

ETYMOLOGY

For Mrs. Mary McClymont of Dalkieth Station who brought the plant fossil locality L717 to the attention of the Queensland Museum.

DIAGNOSIS

Narrow ovate to lanceolate pinnules, base cuneate acute to cuneate obtuse, apex pointed acute, margin serrulate or rarely lobed with 1-2 veins per marginal tooth. Rachilla slender, persistent, giving off regular once or twice dichotomous straight or gently curved lateral veins in subopposite to alternate arrangement at 20°-50°, rarely arching in outer lamina to 70°.

DESCRIPTION

Detached pinnules <39mm long, <18mm wide. Pinnules narrow ovate to lanceolate, base cuneate acute to cuneate obtuse (Fig. 3A,C,E-H), apex pointed acute, margin serrulate (dentation depth <0.5mm; 10-15 teeth per 10mm of margin) with 1-2 veins per marginal tooth (Fig. 3D,H). Margin divided into lobes in some specimens (Fig. 3B,G). Where present, lobes incorporate 2-5 ultimate veins and are separated by notches extending <1/3 distance to midrib, <2mm wide. Rachilla slender (<0.5mm wide), persistent, giving off regular once or twice dichotomous straight or gently curved lateral veins in subopposite to alternate arrangement at 20°-50° (more acute towards apex), rarely arching in outer lamina to 70° (Fig. 2A-D). Each lateral vein terminates in a distally flexed marginal cusp <1mm long, <1mm

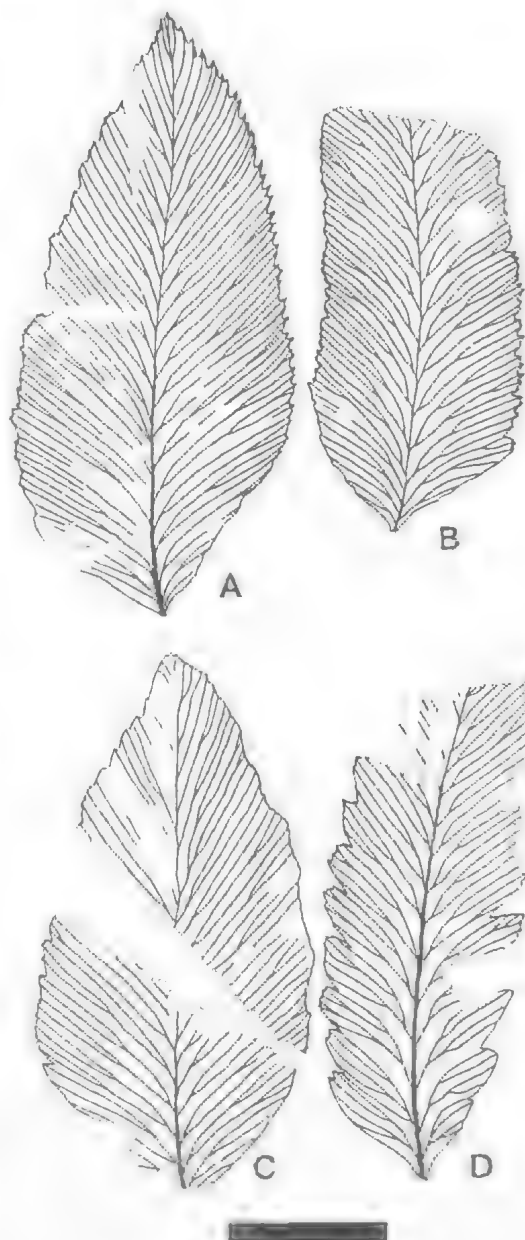


FIG. 2. Line drawings of *Phyllopteroides macclymontae* sp. nov. pinnules showing details of venation and lamina margin. A, QMF32543. B, QMF32594. C, QMF32597. D, QMF32595. All specimens from L717. Scale bar: 1 cm for all illustrations.

wide. Lateral vein density 12-23 per cm at margin. No fertile material available.

COMPARISON AND REMARKS

All preserved pinnae have been detached from the frond at the base of the lamina (no petiole is preserved). Etheridge (1893) established *Phyllopteris feistmanteli* for Late Cretaceous *Phyllopteroides* pinnules from the Cooper Creek area of South Australia and Early Cretaceous specimens from Stewart Creek in Queensland. Specimens from the latter site were transferred to *P. laevis* by Cantrill & Webb (1987). The Cooper Creek specimens are apparently lost (Cantrill & Webb, 1987) but may be coeval with the Winton material based on the distribution of exposed Late Cretaceous strata in the Cooper Creek area (Cowley & Freeman, 1993). The only illustrated Cooper Creek specimen (Etheridge, 1893: fig. 1) shows the basal portion of a leaf with an entire or slightly undulate margin unlike the Winton leaves. Further comparisons are not possible and the status of Etheridge's (1893) species remains uncertain.

Phyllopteroides macclymontae differs from *P. laevis* by its pointed acute apex (Fig. 3A,D) and commonly by its more acute secondary vein insertion angle. *Phyllopteroides laevis* is also a longer leaf, commonly reaching 70mm. *Phyllopteroides serrata* Cantrill & Webb 1987 is closely comparable to *P. macclymontae* on most morphological criteria but the latter appears to have a more regularly serrulate margin with typically one (rarely two) veins per marginal tooth rather than 2-3 veins per tooth in the former species. *Phyllopteroides macclymontae* also has a more distinctly acute apex.

Phyllopteroides lanceolata (Walkom) Medwell 1954 is distinguished from the Winton Formation pinnules by its lesser vein density, typically greater number of veins per marginal tooth (where these are present), and usually by its lesser marginal vein angle. *Phyllopteroides dentata* Medwell 1954 typically has more slender pinnules than *P. macclymontae*, together with a greater dentation depth, lesser concentration of marginal teeth, and greater number of marginal veins per tooth. Day (1964) reported *Phy-*

lopteroides leaves from the Bungil Formation (late Neocomian to early Aptian), Surat Basin, but provided no illustrations or descriptions of that material. However, Cantrill and Webb (1987) assigned Day's (1964) specimens to *P. laevis*. Western Australian Early Cretaceous *Phyllopteroides* pinnules (McLoughlin, in press) generally lack marginal teeth and are more slender than *P. macclymontae*. Cantrill & Webb (1987) indicated that the Queensland specimens assigned to *Phyllopteroides expansa* (Walkom) Medwell 1954b are probably referable to *Sphenopteris*. Leaves referred to *P. expansa* and *P. lanceolata* from the Lower Senonian of New Zealand (McQueen, 1956) are comparable to *P. lanceolata* and *P. serrata* on the basis of their lanceolate-elliptical shape and multi-veined marginal teeth. These features together with their more rounded pinnule apices differentiate the New Zealand specimens from *P. macclymontae*.

The evolutionary relationship between *P. macclymontae* (of Cenomanian age) and the lineages of eastern Australian Early Cretaceous *Phyllopteroides* species proposed by Cantrill & Webb (1987) is unclear. The reduced venation angle of *P. macclymontae* might suggest derivation through the *P. laevis* - *P. serrata* - *P. dentata* lineage. However, the relatively high venation and dentition density and few veins per marginal tooth might indicate an origin via the *P. laevis* - *P. serrata* - *P. lanceolata* lineage.

No sporangiate osmundaceous remains were found in the Winton Formation assemblages prohibiting comparisons with fertile remains assigned to *Cacumen expansa* Cantrill & Webb 1987 associated with *P. dentata* foliage in the Otway Basin.

Family GLEICHENIACEAE

Microphylopteris Arber, 1917

Microphylopteris sp. cf. *M. gleichenioides* (Oldham & Morris) Walkom, 1919 (Fig. 4C,D)

MATERIAL EXAMINED
L552: QMF32477.

overleaf on p. 5

FIG. 3. *Phyllopteroides macclymontae* sp. nov. A. QMF32543, holotype showing spear-shaped pinnule, x 2. B. QMF32533, slender pinnule with lobed margin, x 2. C. QMF32574, small pinnule with slightly sinuous midrib, x 3. D. QMF32543, enlargement of holotype's apex showing one vein per marginal tooth, x 3. E. QMF32514, pinnule with broadly divergent basal lamina margins, x 3. F. QMF32597, hastate pinnule, x 3. G. QMF32595, pinnule with lobed margin, x 3. H. QMF32594, pinnule with finely toothed margin, x 3. All specimens from L717.

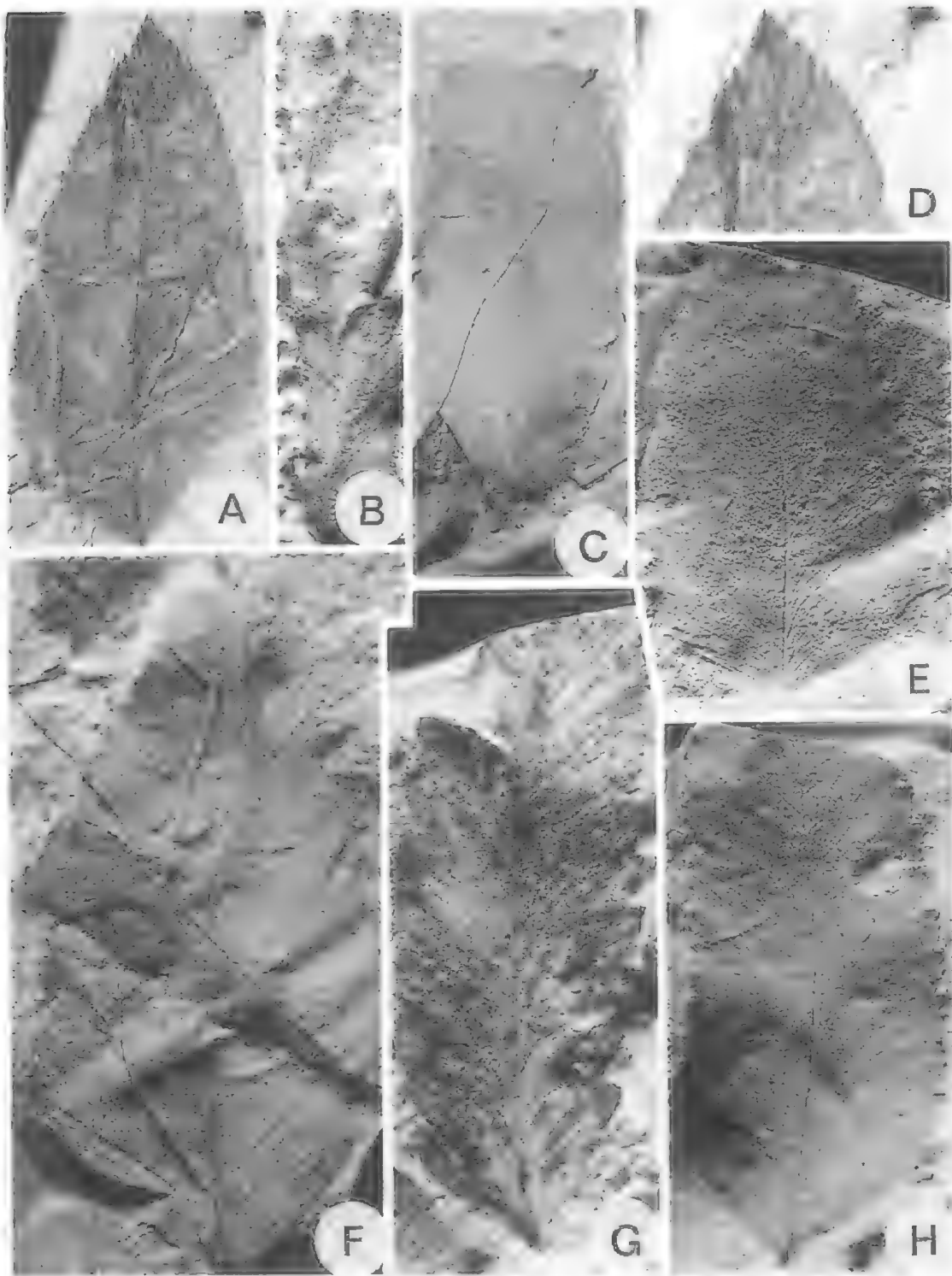


FIG. 3.

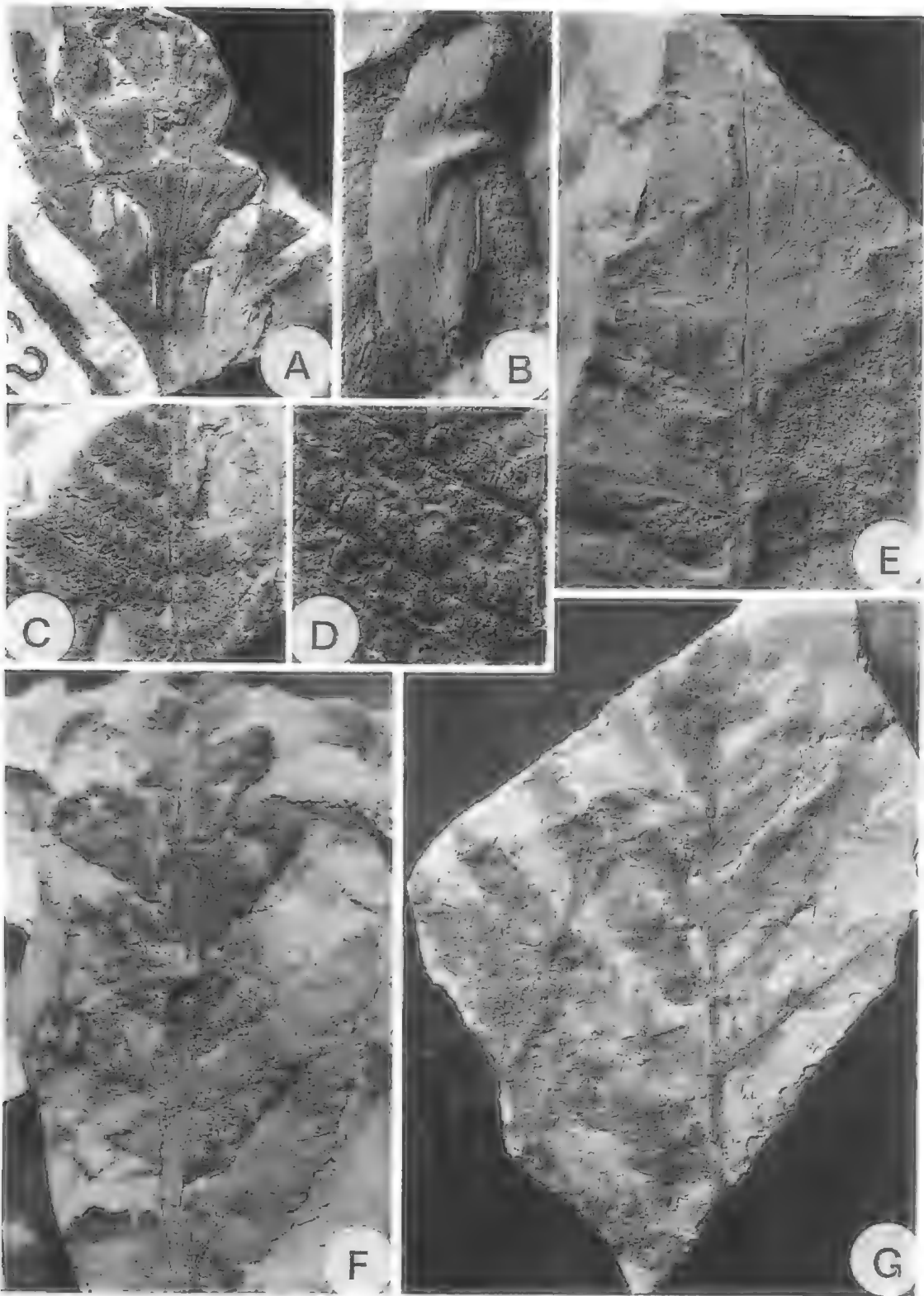


FIG. 4.

DESCRIPTION

Frond at least bipinnate, base and apex absent. Rachis slender (<1mm wide) expanded slightly where pinnae emerge. Pinnae opposite to subopposite, linear or gently falcate, bearing small elliptical, semi-circular, or oblong pinnules in subopposite to alternate arrangement. Pinnae reaching 2.5mm wide and >13mm long, depart rachis at 60°-70° (Fig. 4C). Pinnules decurrent, basiscopic margin strongly rounded (convex), apex rounded or truncate, acroscopic margin slightly convex, straight, or slightly concave, venation indistinct. Pinnules arched dorsoventrally (cup-shaped), reaching 1.5mm long and 1.2mm wide, departing rachilla at 60°-90° (Fig. 4D). Fertile material unavailable.

COMPARISON AND REMARKS

The single fragmentary specimen is insufficient for unequivocal specific identification. The numerous diminutive semi-circular to oblong cup-shaped pinnules with full basal attachment inserted on linear wide-angled pinnae (Fig. 4C,D) is suggestive of a gleicheniacean affinity. *Microphylopteris gleichenioides* (Oldham & Morris) Walkom 1919 occurs in several Australian Late Jurassic and Early Cretaceous assemblages (Gould, 1974; Walkom, 1919a, 1928; White, 1961b). This species is also common in Early Cretaceous Indian (Rajmahal and Jabalpur Formations) fossil suites (Seward & Sahni, 1920; Sah, 1965; Bose & Sah, 1968; Sukh-Dev, 1987). The Late Cretaceous Winton Formation specimen, although very incomplete, is closely comparable to *M. gleichenioides* on the basis of its small, slightly inclined, semi-circular pinnules, and linear pinnae arranged at high angles to the rachis.

Microphylopteris pectinata (Hector) Arber 1917 from the Jurassic and Lower Cretaceous of New Zealand and Australia (Arber, 1917; Walkom, 1919b) has substantially larger pinnae (>8cm) and pinnules (ca. 6mm long). *Gleichenites nanopinnatus* (Douglas) Drinnan & Chambers 1986 differs by its basally contracted, flabellate, and often lobed pinnules.

Gleichenia nordenskiöldii Heer 1874 of Sukh-Dev (1970) from the Lower Cretaceous (Jabalpur Formation) of India is distinguished from the Winton specimen by its expanded basal pinnule margins. The mid-Jurassic *Gleichenites juliensis* Herbst 1962 from Patagonia (Matildean beds) is distinguished by its proportionately more elongate pinnules. *Gleichenites sanmartinii* Halle emend. Herbst 1962 from the Aptian of Argentina (Kachaike Formation) has a superficially similar frond morphology to *M.* sp. cf. *M. gleichenioides* but differs by the contracted bases of its pinnules (Longobucco et al., 1985). However, Herbst's (1962) *G. sanmartinii* specimens from the Argentinian Early Cretaceous (Baqueró Formation) show pinnules with full basal attachment. They typically show pinnules arranged perpendicular to the rachilla but without the apical inclination evident in the Winton specimen. *Gleichenites vegagrandis* Herbst 1962 from the same Argentinian formation, however, does show apically inclined pinnules that are difficult to distinguish from the Queensland material. *Gleichenites* cf. *sanmartinii* of Arrondo & Petriella (1980) from the Early Jurassic of Argentina is also closely comparable to the Winton specimen although the details of pinnule attachments on the former are not clear.

Family UNCERTAIN

Cladophlebis Brongniart, 1849
Cladophlebis sp.
(Fig. 4F,G)

MATERIAL EXAMINED

L552: QMF32465, QMF32466, QMF32467. L717: QMF32626, QMF32627.

DESCRIPTION

Frond at least bipinnate. Base and apex absent in all specimens. Rachis prominent (3mm wide) tapering towards apex. Pinnae opposite to subopposite, lanceolate-lorate, reaching 65mm long, 18mm wide, inserted at 40°-70° to rachis. Pinnules falcate, apex acute, full basal attachment,

previous page

FIG. 4. Ferns. A, QMF32476, *Sphenopteris* sp. cf. *S. warragulensis* McCoy 1892, fragmentary frond, x 2, L552. B, QMF32558, indeterminate fern pinnule, x 3, L717. C, QMF32477, *Microphylopteris* sp. cf. *M. gleichenioides* (Oldham & Morris) Walkom 1919, fragmentary frond, x 2, L552. D, QMF32477, enlargement of pinnules in Fig. 4C, x 6, L552. E, QMF32505, *Sphenopteris* sp., fragment of frond with slender lanceolate pinnules, x 3, L717. F, QMF32465, *Cladophlebis* sp., apical portion of frond with variably lobed pinnules, x 2, L552. G, QMF32467, *Cladophlebis* sp., portion of large frond with opposite to sub-opposite pinnae and falcate pinnules, x 1, L552.

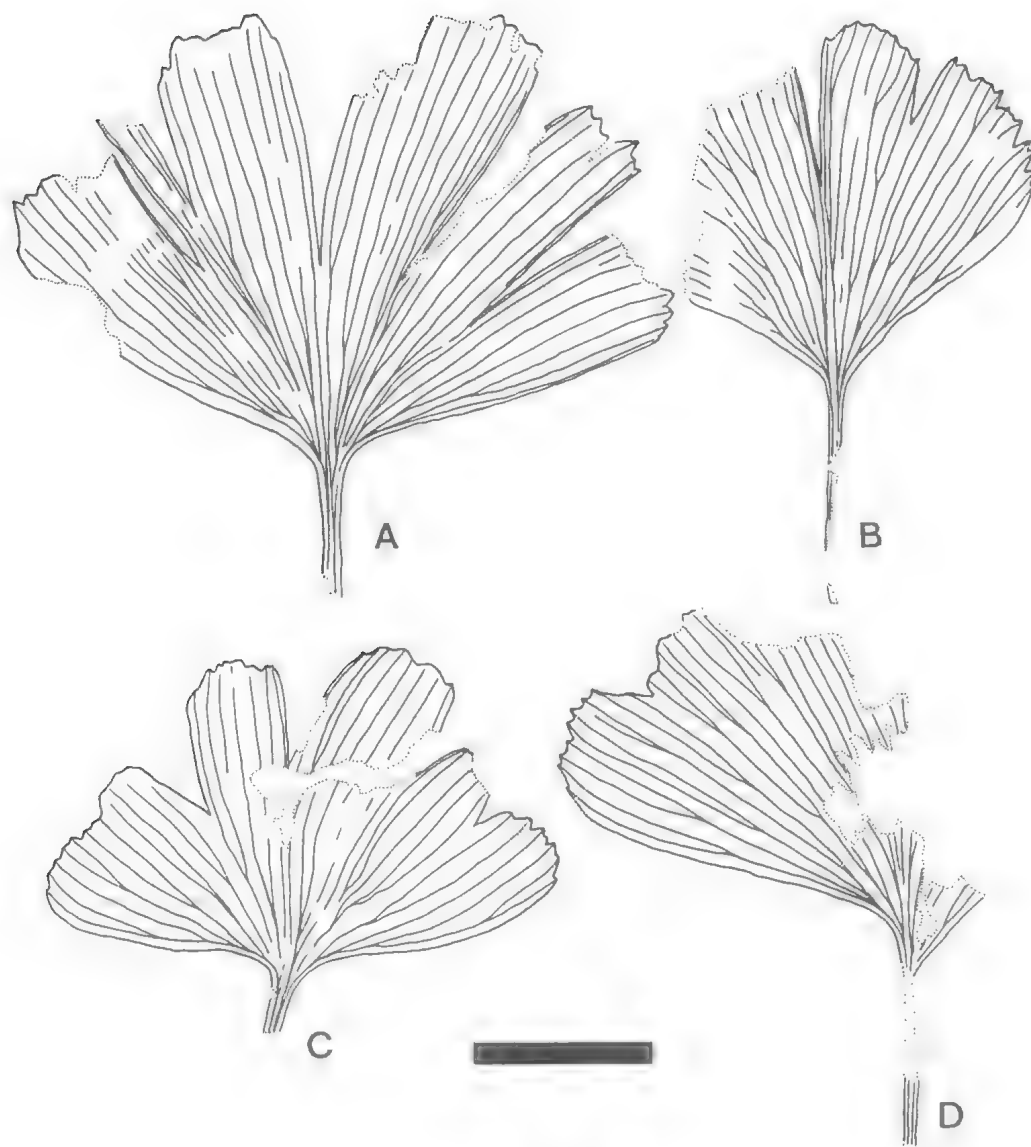


FIG. 5. Line drawings of *Ginkgo wintonensis* sp. nov. A, QMF32478. B, QMF32480. C, QMF32560. D, QMF32525. All specimens from L717. Scale bar: 1cm for all illustrations.

slightly decurrent and connected basally (pinnatisect). Pinnules reaching 22mm long, 6mm wide. Pinnule midribs persistent. Slightly sinuous alter-

nately inserted lateral veins may dichotomize once or twice before margin. Pinnules inserted at 40°-50° to rachilla. No fertile material available.

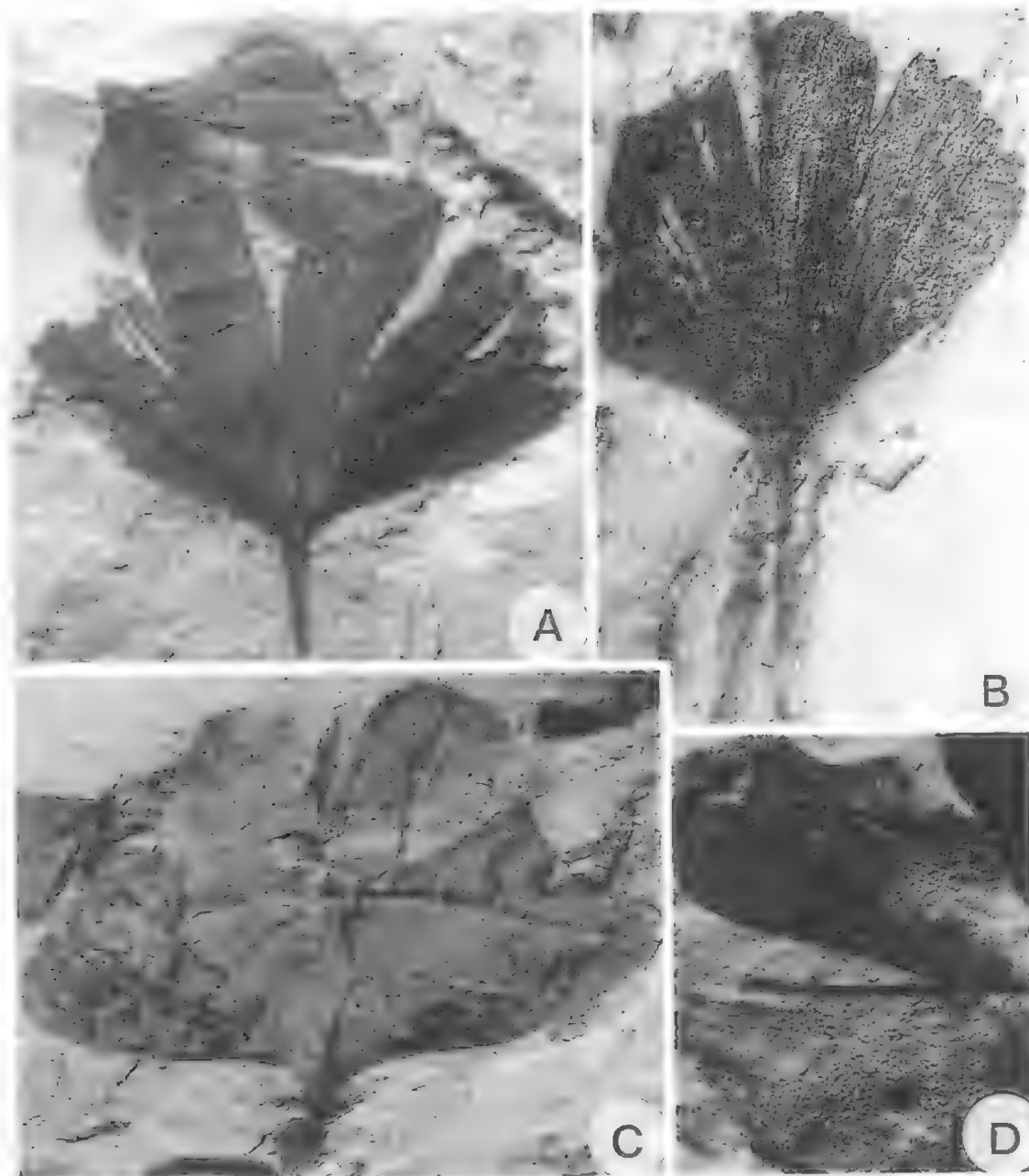


FIG. 6. *Ginkgo wintonensis* sp. nov. A, QMF32478, holotype showing moderately dissected lamina, x 2. B, QMF32480, leaf with minor dissection and long petiole, x 3. C, QMF32560, leaf with broadly divergent basal lamina margin and only minor distal dissection, x 3. D, QMF32525, fragment of leaf showing long petiole, x 2. All specimens from L717.

COMPARISON AND REMARKS

The studied specimens show differing pinna and pinnule shapes according to their position on the parent frond (Fig. 4F,G). As a consequence, individual pinnae and pinnules are comparable to

a range of Mesozoic *Cladophlebis* species described from various Gondwanan provinces. Discovery of more complete fronds may prove some of these species to be synonymous. The Winton fronds are similar to the long-ranging Mesozoic

species *Cladophlebis australis* (Morris) Seward in their entire or gently lobed, falcate, acutely pointed pinnules although pinnules of the former are mostly shorter (Walkom, 1917, 1919a, b; Hill et al., 1966). The Victorian Early Cretaceous species *Cladophlebis biformis* Drinnan & Chambers 1986 and *C. sp. cf. C. oblonga* Halle 1913 also have proportionately longer entire-margined pinnules.

Specimens assigned to *Coniopteris ?lobata* (Oldham) by McQueen (1956) from the New Zealand Upper Cretaceous show pinnule variation similar to that of the Winton fronds but the former typically have more rounded and lobed pinnule apices.

Amongst the Indian forms, *Cladophlebis sp.* differs from *C. srivastavae* Gupta 1955 by its substantially larger pinnules (Gupta, 1955). *Todites indicus* (Oldham & Morris) Bose & Sah 1968 fronds differ only in their more sharply pointed pinnules. No fertile fronds are available amongst the Winton specimens to permit comparison with the sporangiate pinnules of *T. indicus*. South African Early Cretaceous fronds assigned to *Cladophlebis* spp. A, B, and C (Anderson & Anderson, 1985) have pinnules with more rounded apices than the Winton specimens.

Family UNCERTAIN

Sphenopteris (Brongniart) Sternberg, 1825
Sphenopteris sp. cf. S. warragulensis
 McCoy, 1892
 (Fig. 4A)

MATERIAL EXAMINED
 L552: QMF32476.

DESCRIPTION

Frond at least bipinnate, base and apex absent. Rachis prominently grooved (on impression).

Pinnae lanceolate-linear, subopposite to alternate, reaching 30mm long, 6mm wide (Fig. 4A). Pinnae inserted on rachis at approximately 30°, straight or gently arched distally. Pinnules lanceolate, reaching 11mm long, 2mm wide, subopposite, decurrent basiscopic margins extending along rachilla to form a narrow wing, inserted on rachilla at 10°-30°. Pinnule midvein persistent, branching several times to produce 3-5 acute, generally unbranched, lateral veins which typically terminate in acute marginal cusps. Initial veins in pinnules catadromous. No fertile material available.

COMPARISON AND REMARKS

The studied specimen closely resembles *Sphenopteris warragulensis* McCoy 1892 from the Victorian Early Cretaceous (Drinnan & Chambers, 1986) although no fertile fronds are available for comparison. Some *S. warragulensis* specimens show a greater degree of pinna dissection than the Winton frond but considerable morphological variation was reported amongst the Victorian foliage fragments according to their original position on the parent frond (Drinnan & Chambers, 1986). *Sphenopteris flabellifolia* Tenison-Woods 1883 from the Maryborough Basin Lower Cretaceous also has markedly dissected lanceolate fronds and may be closely allied to both *S. warragulensis* and the Winton frond. *Sphenopteris travisi* Stirling 1900 and *Sphenopteris sp.* of Drinnan & Chambers (1986) from the Victorian Lower Cretaceous both differ from the Winton specimen by their substantially shorter and more ovate to elliptical pinnae. Similarly, *S. erecta* (Tenison-Woods) Walkom 1919 has proportionately shorter rhomboid pinnules than *S. sp. cf. S. warragulensis*.

overleaf on p.284

FIG. 7. *Araucaria sp. cf. A. mesozoica* Walkom 1918. A, QMF32542, robust twig with broad elliptical leaves, x 1, L717. B, QMF32572, slender twig with narrow lanceolate leaves, x 1, L717. C, QMF32578, longitudinally fractured mould of robust twig showing arched, spirally arranged, scale-like leaves, x 1, L406. D, QMF32484, slender twig with intermediate-sized lanceolate leaves, x 1, L717. E, F32488, slender twig with linear leaves twisted to lie in a common plane, x 1, L717.

overleaf on p.285

FIG. 8. A-C, *Araucarian microsporangiate cones*; D-F, *Araucaria sp. cf. A. mesozoica* Walkom 1918 foliage. A, QMF32598, arched cone with densely crowded microsporophylls, x 2, L717. B, QMF32499, cone with lax peltate or elongate rhomboid microsporophylls, x 2, L717. C, QMF32446, cone showing axis with spirally arranged microsporophyll scars, x 5; L406. D, QMF32535, broad leaf with attenuate apex, x 1, L717. E, QMF32442, robust axis showing spirally arranged, broad, lanceolate leaves with broadly elliptical attachments, x 1.5, L406. F, QMF32561, slender twig bearing two ranks of narrow lanceolate leaves, x 1.5, L717.

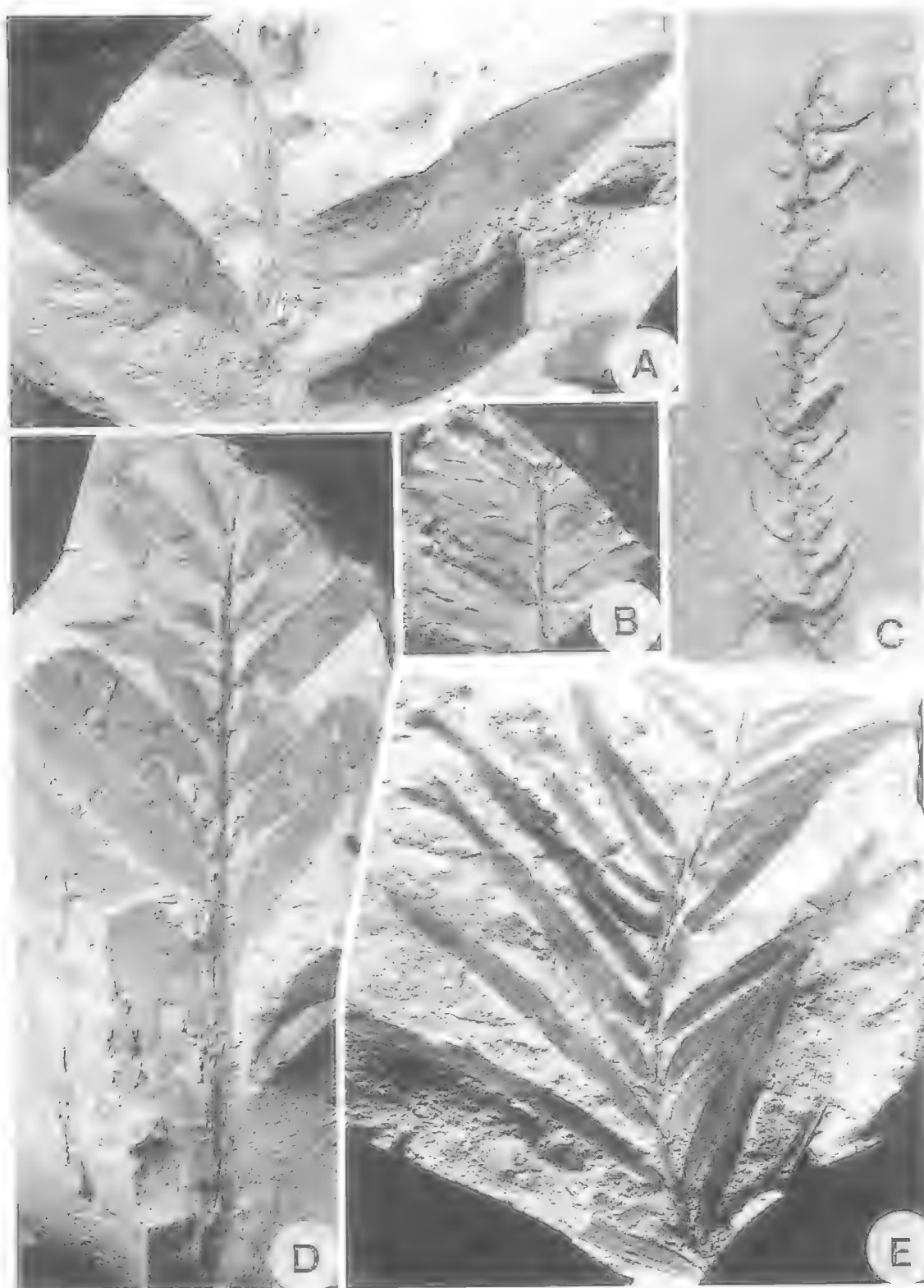


FIG. 7

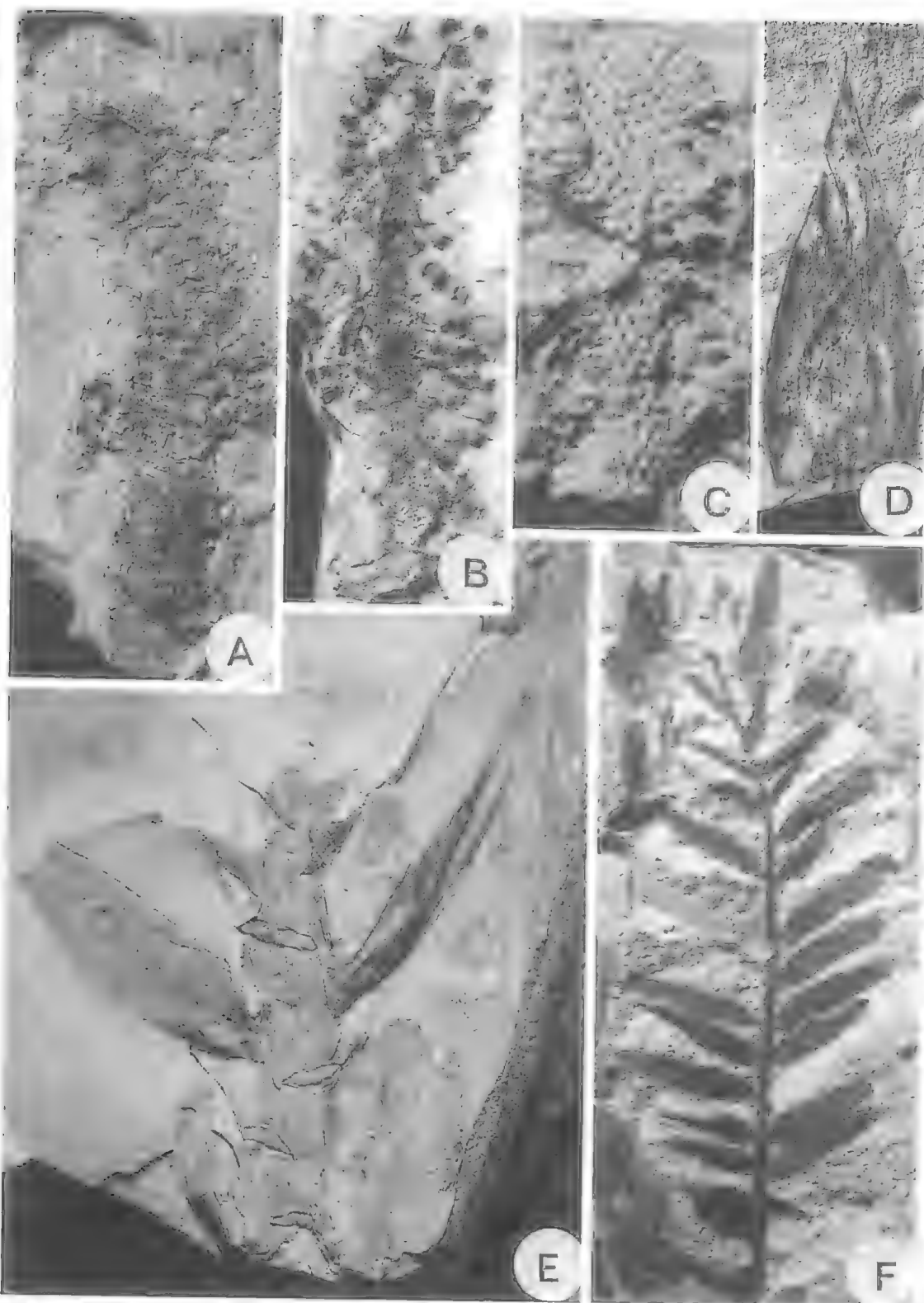
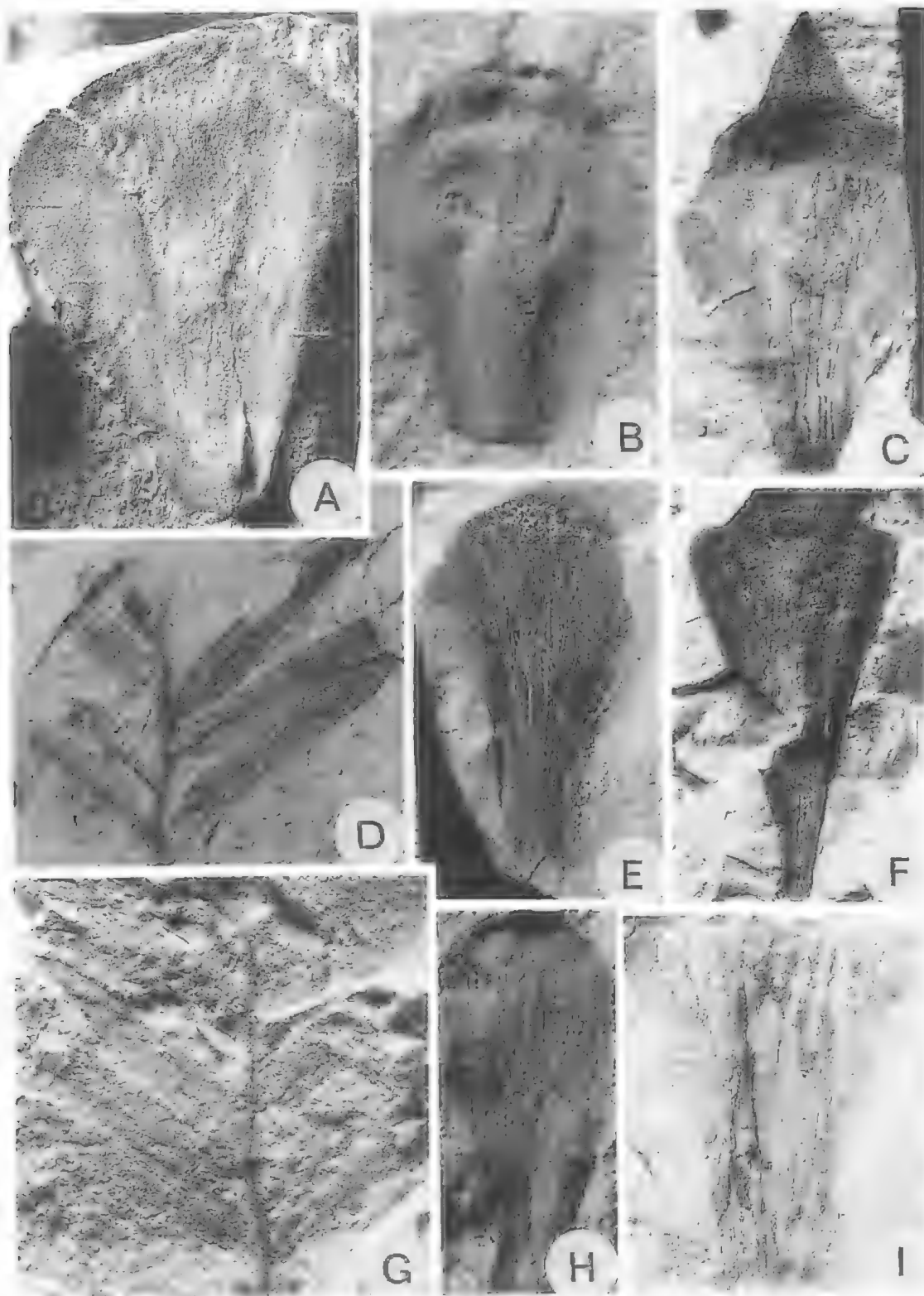


FIG. 8



***Sphenopteris* sp.**
(Fig. 4E)

MATERIAL EXAMINED
L717: QMF32505.

DESCRIPTION

Frond at least bipinnate, base and apex absent. Rachis prominently grooved (on impression), flanked by a slender (<0.5mm) wing. Pinnae ovate-elliptical, alternate, reaching >11mm long, 5mm wide. Pinnae inserted on rachis at 40°–60°, straight or gently arched distally. Pinnules linear-lanceolate, reaching 5mm long, 1mm wide, alternate, basiscopic margins decurrent, inserted on rachilla at 30°–40° (Fig. 4E). Pinnule midvein persistent?, lateral veins indistinct. Initial veins in pinnae catadromous. No fertile material available.

COMPARISON AND REMARKS

The single indistinct frond impression reveals little detail for comparison to previously illustrated ferns. The small pinnae dissected into slender pinnules (Fig. 4E) are reminiscent of several *Sphenopteris* species. The lanceolate pinnules of the studied specimen serve to differentiate it from the ovate, lobed pinnules of *S. travisi* Stirling 1900 and *Sphenopteris* sp. (Drinnan & Chambers, 1986) from the Victorian Early Cretaceous. White's (1961a) "*Stenopteris tripinnata* Walkom" from the Early Cretaceous Cronin Sandstone, Officer Basin, Western Australia, has pinnae dissected into linear pinnules although neither the Western Australian nor Winton Formation specimens are sufficiently complete or well-preserved to confirm synonymy. Zeba-Bano's (1980) *Sphenopteris* sp. B from the Early Cretaceous Jabalpur Formation, India, has slightly more elongate pinnae with slender obovate pinnules.

Indeterminate fern pinnule
(Fig. 4B)

MATERIAL EXAMINED
L717: QMF32558.

REMARKS

A single detached pinnule (Fig. 4B) from L717 may belong to a cladophleboid or sphenopterid fern. The pinnule is 18mm long, 6mm wide, lanceolate, with a slightly undulate margin. The pinnule midrib is sinuous, giving off sub-opposite to alternate, once-dichotomous, lateral veins at 20°–30°. Each lateral vein terminates in a short, blunt, marginal tooth. The pinnule shares characters with a number of Gondwanan *Cladophlebis* and *Sphenopteris* species but cannot be reliably assigned to either taxon owing to its incomplete preservation.

Phylum GINKGOPHYTA
Class GINKGOOPSIDA
Order GINKGOALES
Family GINKGOACEAE

Ginkgo Linnaeus, 1771
Ginkgo wintonensis sp. nov.
(Figs 5A–D, 6A–D)

MATERIAL EXAMINED

HOLOTYPE: L717: QMF32478.
PARATYPES: L717: QMF32479, QMF32480, QMF32496, QMF32525, QMF32537, QMF32560, QMF32561, QMF32620, QMF32622, QMF32623.

ETYMOLOGY

After the host formation.

DIAGNOSIS

Petiolate, flabellate leaves symmetrical about the petiolar axis. Distal lamina margin undulate to serrulate with one to five principle clefts incised to less than three fifths of the lamina width. Petiole <24mm long, <1mm wide, expanding into the lamina with a basal angle of 120°–180°. Venation gently divergent, dichotomizing <5 times chiefly in the proximal half of lamina, veins terminating in short marginal teeth.

DESCRIPTION

Leaf simple, petiolate, lamina 20–37mm wide, 17–30mm long. Leaves symmetrical about the petiolar axis. Petiole 12–24mm long, <1mm wide (Figs 5B,D; 6B,D). Lamina flabellate, dissected, basal angle 120°–180°. Major dissection, along

FIG. 9. A–C, E, F, H, I, Araucarian ovulate cone scales: D–G, cf. *Elatocladus plana* (Feistmantel) Seward 1918. A, QMF32482, broadly rounded scale, x 2, L717. B, QMF32447, broadly rounded scale with short spine, x 4, L406. C, QMF32540, scale with prominent venation and large apical spine, x 3, L717. D, QMF32515b, slender twig bearing oblong leaves with contracted bases, x 3, L717. E, F32502, scale with prominent dichotomous venation, x 2, L717. F, QMF32494, deltoid scale, x 2, L717. G, QMF32515a, counterpart to Fig 9D, x 3, L717. H, QMF32444, club-shaped scale, x 4, L406. I, QMF32563, scale with prominent venation, x 2, L717.

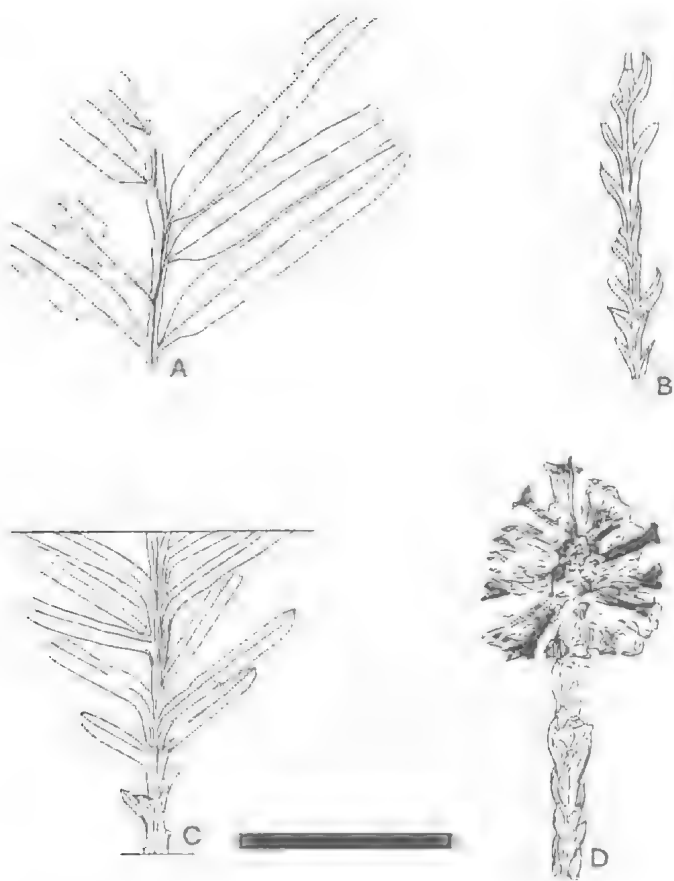


FIG. 10. Line drawings of selected Winton Formation conifer remains showing variation in leaf types. A, QMF32515b, cf. *Elatocladus plana* (Feistmantel) Seward 1918. B, QMF32491, cf. *Austrosequoia wintonensis* Peters & Christophel 1978, terminal portion of twig with arched scale-like leaves. C, QMF32564, Conifer sp. A. D, QMF32550, cf. *Austrosequoia wintonensis* Peters & Christophel 1978, axis with adpressed scale-like leaves and terminal cone. Scale bar; 1cm.

centre of leaf, $1/3 - 3/5$ width of lamina (Figs 5A,B; 6A,B). One to two dissections on either side of major dissection, incised $1/7 - 1/3$ width of lamina (Figs 5A-C; 6A-C). Venation gently divergent (Fig. 5A-D). Two veins emerge from petiole and bifurcate <5 times in proximal half of lamina, rarely bifurcating in outer lamina. Distal lamina margin undulate to serrulate, veins terminating in short (<1 mm) marginal teeth (Fig. 5B).

COMPARISON AND REMARKS

Fertile material and attached axes are unavailable for the Winton material. *Ginkgo australis* (McCoy) Drinnan & Chambers 1986 from the

Australian Early Cretaceous and the morphologically similar *Ginkgoites tigrensis* Archangelsky 1965 and *Ginkgoites ticoensis* Archangelsky 1965 from coeval South American strata (Archangelsky, 1965) differ from *Ginkgo wintonensis* sp. nov. by their generally larger lamina radius, more deeply dissected lamina, and narrower lamina segments. Walkom's (1918, 1919a) *Ginkgo digitata* (Brongniart) from the Maryborough Formation and Burrum Coal Measures, Maryborough Basin, is a smaller leaf form with a lesser degree of lamina dissection than *G. australis* but similar to *G. wintonensis*. However, Walkom (1919a) indicated that the Maryborough Basin specimens displayed a considerable range of leaf morphologies. Walkom's specimens show a lesser angle of basal lamina divergence from the petiole than do the Winton Formation specimens. The affinities of Walkom's (1918, 1919a) Maryborough Basin leaves will remain uncertain until better material is available.

Ginkgoites waarrensis Douglas 1965 from ?Cenomanian strata of Victoria was defined substantially on cuticular information as only a few incomplete leaves were available from bore core material. Douglas (1965) illustrated two macrofossil specimens at least one of which shows a petiolate leaf with a lamina dissected almost to its base. *Ginkgo wintonensis* leaves

from probable coeval Queensland strata show a lesser degree of lamina dissection but further comparisons are not possible owing to the lack of cuticular detail on the Winton specimens.

Fragmentary foliage assigned by Seward & Sahni (1920) to *Ginkgoites lobata* (Feistmantel) Seward and *Ginkgoites crassipes* (Feistmantel) Seward from the Indian Lower Cretaceous are similarly small leaves with comparable lamina dissection to *Ginkgo wintonensis* although the Indian forms show a lesser angle between the base of the lamina and the leaf midline. *Ginkgo rajmahalensis* (Sah & Jain) Zeba-Bano,

Maheshwari & Bose 1979 from the Indian Early Cretaceous incorporates substantially larger or more deeply dissected leaves than *G. wintonensis* (Sah, 1953; Mehta & Sud, 1953; Sah & Jain, 1965; Zeba-Bano et al., 1979). *Ginkgoites feistmantelii* Bose & Sukh Dev 1960, another Indian Early Cretaceous species, differs by its entire margin or very minor medial lamina cleft.

Ginkgoites waarrensis and *Ginkgo wintonensis* represent the youngest macrofossil examples yet recorded within Australia of the previously widespread and abundant ginkgoalean clade. Leaves of these Late Cretaceous ginkgoaleans are typically smaller than early Mesozoic Australian representatives but are otherwise similar in general morphology. Early Cretaceous Victorian and mid-Cretaceous Winton Formation ginkgoalean leaves were abscised whole (Drinnan & Chambers, 1986) and like the extant *Ginkgo biloba* were probably borne by deciduous plants. No major climatic changes have been invoked for the relatively high latitude Australian region during the Late Cretaceous (Dettmann et al., 1992). The causes for the extinction of ginkgoaleans from the Australian vegetation during the Late Cretaceous (together with pentoxyleans, bennettitaleans, and equisetaleans) remain unclear although competition from the rapidly diversifying angiosperms may have played a role in their demise.

Phylum CONIFEROPHYTA
Class CONIFEROPSIDA
Order CONIFERALES
Family ARAUCARIACEAE

Araucaria Jussieu, 1789

Araucaria sp. cf. *A. mesozoica* Walkom, 1918
(Figs 7A-E, 8D-F)

Podozamites sp.; White, 1974: 2, fig. 4 (in part).

Equisetites sp.; White, 1974: 2, fig. 4 (in part).

Branchlet (Araucariaceae); Dettmann et al. 1992: fig. 15d.

MATERIAL EXAMINED

L406: QMF32440-3, QMF32576, QMF32578, QMF32599, L717: QMF32484, QMF32488, QMF32498, QMF32501, QMF32516, QMF32518, QMF32528, QMF32534, QMF32535, QMF32541, QMF32542, QMF32549, QMF32572, QMF32575, QMF32600-2, QMF32606, QMF32607, QMF32634.

DESCRIPTION

Fragmentary shoots reaching 13cm long, 1cm wide, bearing spirally arranged scale-like rhomboid (Fig. 7C), elliptical (Fig. 7A), or lanceolate (Figs 7B,D,E; 8E,F) leaves. Leaf dimensions and orientation vary in a sequential (seasonal?) manner along the axis. Larger (lanceolate) leaves typically twisted at base to lie roughly in a common plane (Figs 7A,B,D,E; 8F). Smaller (scale-like) leaves apparently maintained in a spiral arrangement (Fig. 7C) although flattened by sediment compaction. Leaves parallel-veined, 12-16 veins per cm across mid-lamina; apex broadly rounded to pointed acute, rarely acuminate (Fig. 8D); bases contracted, leaving a transversely elliptical, slit-like, or crescentic scar when detached (Fig. 8E). Leaves reaching >10cm long and 25mm wide. Leaf length:width ratio 1.5:1 to 15:1. Beyond basal flexure leaves are straight, gently curved distally, or reflexed; typically arrayed at 40-90° to axis.

COMPARISON AND REMARKS

Foliage-bearing axes of this species represent the most robust conifer remains from the Winton Formation. The largest specimen from L406 illustrated by Dettmann et al. (1992, fig. 15d) shows three attached branchlets with leaves varying from short spine-like or triangular scale-like forms to more typical linear examples in a repeated manner along the axes. Such lamina variation is evident on axes of the extant Bunya Pine (*Araucaria bidwillii*) and is a consequence of climatic seasonality. Of the extant Australasian araucarians, the Winton specimens are most comparable to *A. bidwillii* in terms of leaf size and seasonal variation but the former typically develop more elongate strap-shaped leaves in each growth cycle. Cone scales associated with the

overleaf on p.290

FIG. 11. cf. *Austrosequoia wintonensis* Peters & Christophel 1978. A, QMF32520, longitudinal imprints of three associated cones, x 2. B, QMF32543, several associated twigs and cones, x 1. C, QMF32530, slender stem with recurved scale-like leaves, x 2. D, QMF32491, slender stem with spirally arranged arched leaves, x 3. E, QMF32528, pair of slender axes with spirally arranged elongate-rhomboid leaf scars, x 4. F, QMF32571, slender stem with owl-shaped leaves, x 3. G, QMF32550, longitudinal imprint of cone borne on stem with spirally arranged scale-like leaves, x 5. H, QMF32536, oblique imprint of cone with peltate scales, x 5. I, QMF32490, slender branched axes associated with cones, x 2. All specimens from L717.

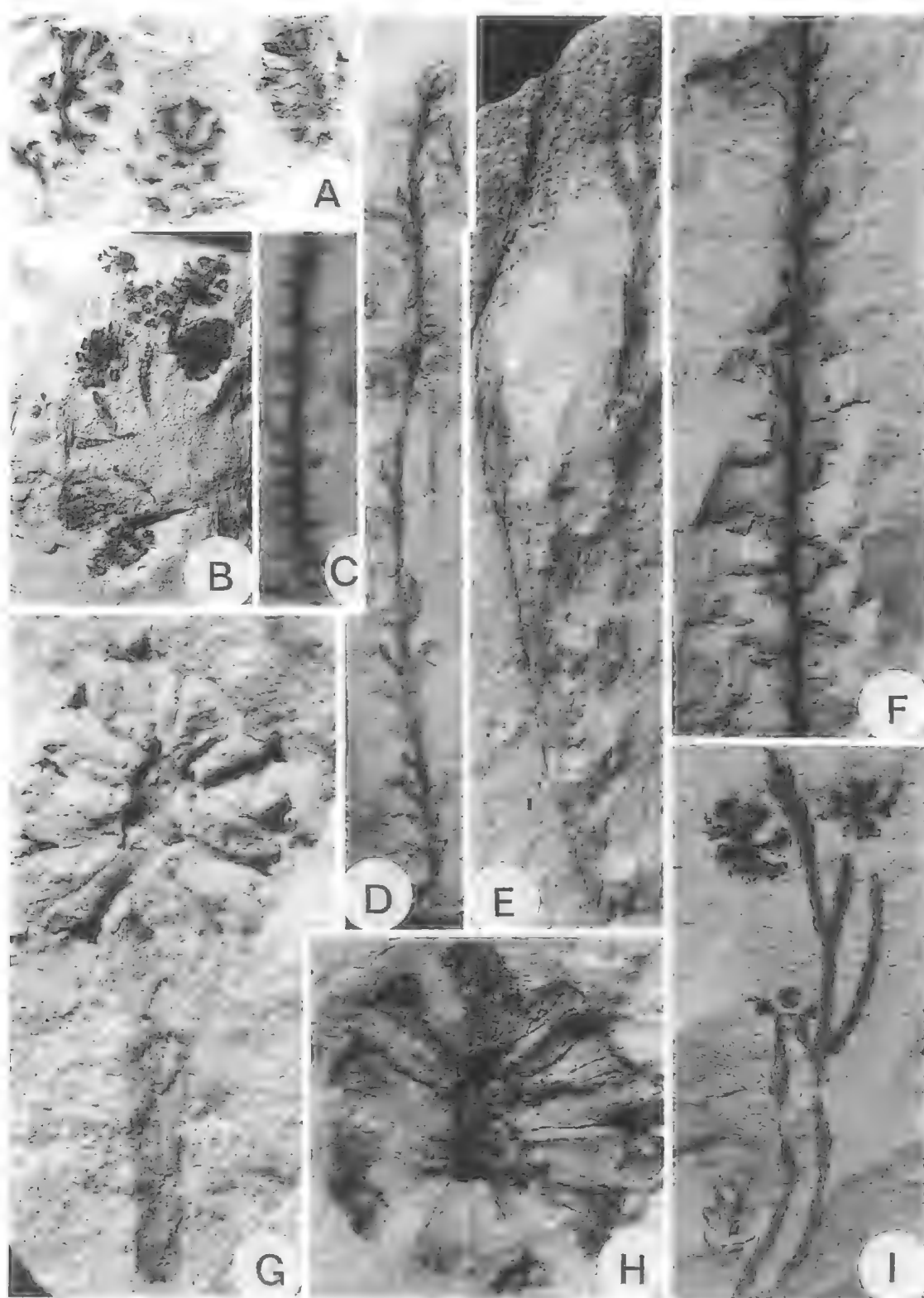


FIG. 11

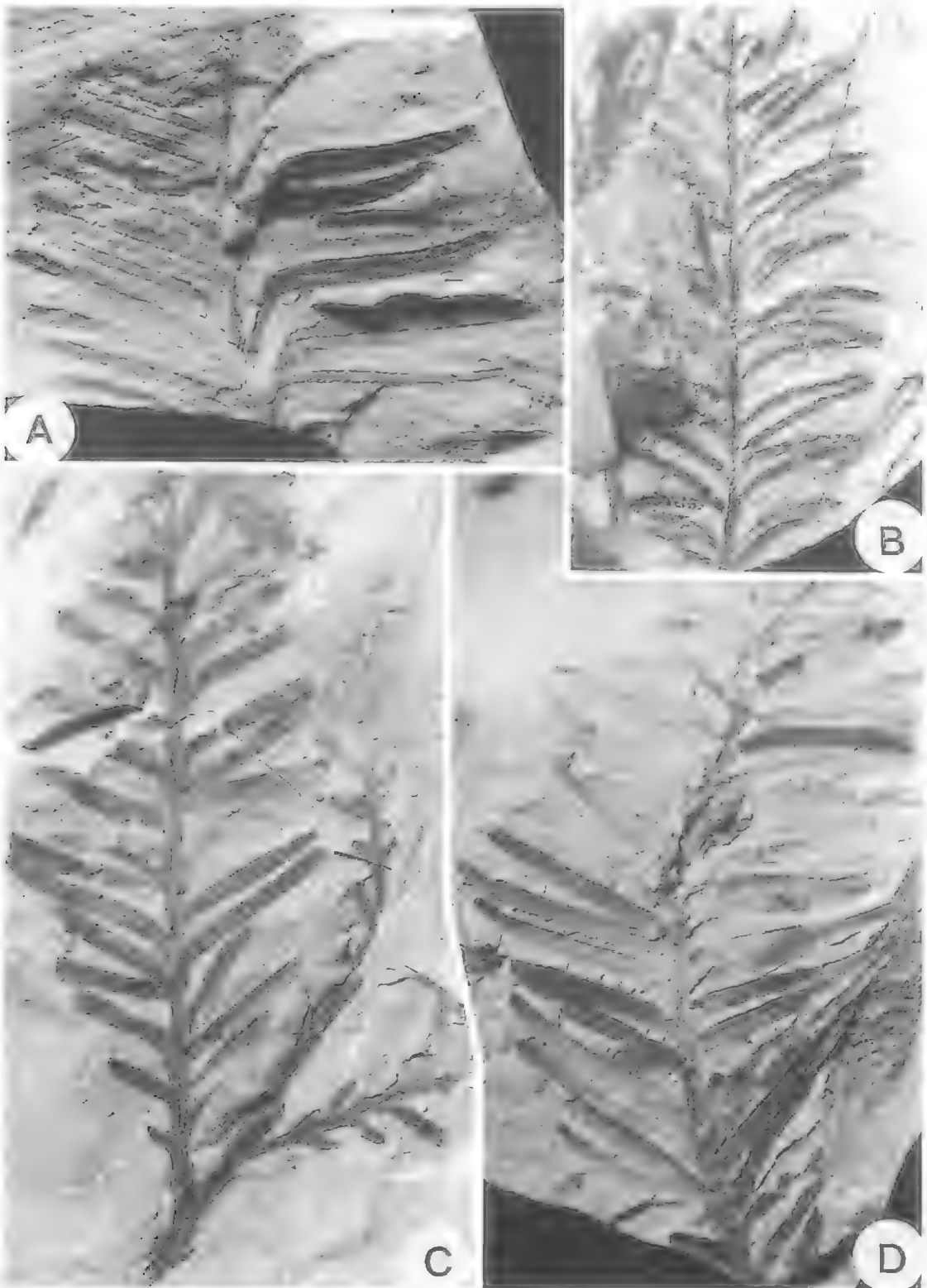


FIG. 12

Winton araucarian foliage are additionally more elongate than *A. bidwillii* scales. *Araucaria cunninghamii* and *A. heterophylla* differ by having consistently smaller scale-like or spine-like leaves. Leaves of the extant New Guinean *Araucaria hunsteinii* differ by their abaxial keel as do leaves of *A. haastii* Ettingshausen emend. Bose from the Late Cretaceous (?Campanian) of New Zealand (Bose, 1975).

Both White's (1974) *Podozamites* sp. and *Equisetites* sp. probably belong to *A.* sp. cf. *A. mesozoica*. Her *Equisetites* sp. appears to represent a detached parallel-veined linear leaflet traversed by several fractures and stain-lines which may have been misinterpreted as nodes.

Walkom's (1919a) *Podozamites kidstoni* Etheridge and *P. lanceolatus* Lindley & Hutton from the Burnum Coal Measures differ from the Winton specimens by their elliptical-oblong leaves with broadly rounded apices. However, his detached leaflets assigned to *Podozamites* sp. have sharply pointed apices similar to the specimens described above. The incompleteness of Walkom's (1919a) *Podozamites* sp. specimen prevents closer comparison although the parallel-veined leaf with a contracted base which he described as *Zamites takuraensis* may belong to the same species. *Araucarites mesozoica* Walkom 1918 has leaves and leaf scars which are very similar to those of the Winton specimens although the few incomplete stems and leaves of this Maryborough Formation species do not show the range of foliar variation evident in examples of the latter. Walkom's (1919b) *Araucarites gracilis* Arber and *Araucarites* sp. from the Jurassic of the Clarence-Moreton Basin, New South Wales, have apically slender and basally tapered two-ranked leaves and may also have close affinities to the Winton specimens. The prominently decurrent bases and narrow laminae of *Podozamites taenioides* Cantrill 1991 serve to distinguish that Victorian Early Cretaceous species from the Winton forms. *Araucaria* sp. cf. *A. heterophylla* (Salisbury) Franco and *Araucaria* sp. of Drinnan & Chambers (1986) from the Victorian Lower Cretaceous differ from the Winton material by their much smaller awl-shaped or imbricate scale-like leaves. The Winton specimens show sufficient variation in their gross foliar morphology to be accommodated within

several araucariacean species (viz., *Araucaria seorsum*, *A. lanceolatus*, *A. acutifolius*, *A. falcatus*, *Agathis victoriensis*) erected by Cantrill (1992) for material from the Victorian Early Cretaceous. Absence of cuticular detail on the Winton specimens prevents critical comparison to Cantrill's (1992) species. *Agathis jurassica* White 1981 from the Middle Jurassic Talbragar Fish Beds differs by its uniform leaves arranged spirally about the stem rather than twisted to form two ranks as shown by the Winton specimens.

New Zealand Late Cretaceous leaves assigned to *Araucarites marshalli* Edwards 1926 are similar to the broader leaves of *Araucaria* sp. cf. *A. mesozoica*. The few and fragmentary specimens of the New Zealand species prevent closer comparison.

Araucarian microsporangiate cones (Fig. 8A-C)

MATERIAL EXAMINED

L406: QMF32446. L717: QMF32492, QMF32499, QMF32532, QMF32538, QMF32598, QMF32603.

DESCRIPTION

Oblong cones reaching 5cm long, 1.7cm wide, consisting of slender (<3mm wide) axis bearing loose, radially disposed distally expanded (peltate?) scales. Scales <7mm long, expanded distally into a 2mm high rhomboid shield. Pollen not preserved.

COMPARISON AND REMARKS

The oblong shape of the cones (Fig. 8A), the diminutive size of the densely spaced, spirally arranged, peltate? bracts (Fig. 8B-C), and their association with ovulate cone scales and araucarian foliage suggests that these organs are araucarian pollen cones. Peters & Christophel (1978, fig. 17) illustrated a permineralized araucarian cone from the Winton Formation with rhomboid scales similar to the impressions described herein. *Araucarties ?polycarpa* Tenison-Woods of Hill et al. (1966) from the Early Cretaceous of the Stanwell Coal Measures is a slightly larger and better preserved cone showing tightly overlapping bracts. The cone is probably pollen-bearing rather than ovulate as proposed by Hill et al. (1966) and, although larger, may have been a

previous page

FIG. 12. Conifer sp. A. A. QMF32522, slender twig bearing basally arched leaves, x 5. B. QMF32481, slender twig bearing gently arched leaves, x 3. C. QMF32564, branched twigs bearing leaves of variable size, x 3. D. QMF32552, slender twig bearing linear univeined leaves in two ranks. All specimens from L717.

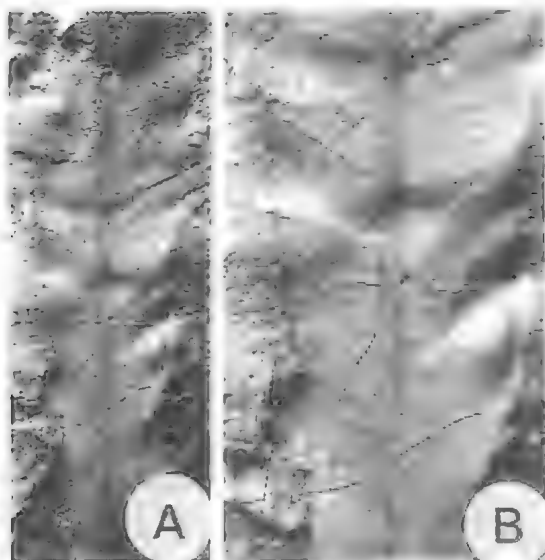


FIG. 13. *Taeniopteris* sp., NMVP199579. A, leaf with prominent midrib and straight secondary veins inserted at 60° to the midvein, x 1. B, details of venation, x 2.

closed immature cone otherwise similar to the Winton specimens. Modern Australian *Araucaria* and *Agathis* species have pollenate cones of similar-shape to the Winton specimens but incomplete preservation and lack of associated pollen with the fossils inhibits closer comparison.

The Winton cones are substantially larger and more oblong than the pollenate cones referred to *Brachyphyllum feistmantelii* and *Nothopheuen brevis* from the Early Cretaceous of Argentina (Baldoni, 1979; del Fueyo, 1991).

***Araucarian ovulate cone scales* (Fig. 9A-C,E,F,H,I)**

Seed cone scales (Araucariaceae). Dettmann et al., 1992: fig. 15e.

MATERIAL EXAMINED

L406: QMF32444, QMF32447. L717: QMF32482, QMF32493, QMF32494, QMF32502, QMF32540, QMF32563.

DESCRIPTION

Triangular-rhomboid cone scales consisting of central triangular strongly vascularized fertile area (Fig. 9A,C,E,I) flanked by marginal poorly vascularized wings. Base tapered but with broad attachment area (Fig. 9C,H); apex varying from broadly rounded to acutely pointed (Fig. 9A-C,E,H); margin entire. Venation divergent di-

chotomous, 10-20 veins per cm adjacent to scale shoulders. Scales 10-37mm long, 7-26mm wide. Shoulders of scales broadly rounded (Fig. 9A) to sharply angled (Fig. 9F). Apical spine <1-5mm long (typically less than one fifth length of scale). Ovule position poorly defined, typically marked by gentle oblong or obovate depression along proximal part of cone scale axis (Fig. 9A,I).

COMPARISON AND REMARKS

All scales are detached although they are sometimes densely clustered on bedding planes. The cone scales display a wide range of sizes and show varying shoulder angles and spine lengths. This variation may be due to their derivation from different plant species, however, the range of shapes and dimensions displayed would not be unexpected within an araucarian species or even within a single cone. The cone scales are commonly associated with foliage of *Araucaria* sp. cf. *A. mesozoica*.

Gondwanan uniovulate conifer cone scales have been assigned to a range of *Araucarites* species based on gross shape, scale dimensions, and prominence of the apical spine. The illustrated differences between many of these species might conceivably be accommodated within an individual cone. We have therefore retained the dispersed Winton cone scales under open nomenclature until attached specimens are found. The most similar Australian cones scales to those presently described are those referred to *Araucarites cutchense* Feistmantel 1876 by Medwell (1954a) and *Araucarites arberi* Walkom 1919a from the Early Cretaceous of Victoria and Queensland (Maryborough Basin) respectively. *Araucarites arberi* has a longer apical spine than the Winton scales but the variation in scale morphology suggests that this may not be a consistent character. Similarly, Medwell's (1954a) specimens fall within the range of morphologies exhibited by the Winton scales.

Family ?PODOCARPACEAE

?*Elatocladus* Halle, 1913
cf. *Elatocladus plana* (Feistmantel)
Seward, 1918
(Figs 9D,G, 10A)

MATERIAL EXAMINED

L717: QMF32515, QMF32613



DESCRIPTION

Slender (<1mm wide) axes with a narrow (<0.5 mm) lateral flange, bearing spirally arranged leaves twisted at their base to lie in a common plane. Leaves univeined, lanceolate to linear, <2mm wide, 10-20mm long. Leaf apex pointed acute; margin entire; base strongly contracted (Fig. 9D,G); petiole negligible. Fructification unknown.

COMPARISON AND REMARKS

This species is distinguished from other conifers in the Winton assemblages by its small, lanceolate to linear univeined leaves, with contracted bases occurring on slender planated branches (Fig. 9d). Similar material from the Gondwanan Jurassic and Cretaceous has frequently been assigned to *Elatocladus confertus* (Oldham & Morris) Halle 1913, *E. heterophylla* Halle, *E. plana* (Feistmantel) Seward, or *Podocarpus* spp. (e.g., Halle, 1913; Arber, 1917; Walkom, 1917; 1919a; 1928; Archangelsky, 1966; Maheshwari & Singh, 1976; Anderson & Anderson, 1985) while Triassic foliage assigned to *Rissikia* species (Townrow, 1967; Anderson & Anderson, 1989) is commonly also similar. In some cases the differences between these taxa are not well-defined and in others (e.g., *E. plana*) foliage of strikingly dissimilar shapes or dimensions has been included in the same species (contrast e.g., Walkom, 1921; White, 1961a; Baksi, 1968). Western Australian Cretaceous forms previously assigned to *E. plana* (Walkom, 1944; White, 1961a) have more needle-like leaves than flattened oblong to linear foliage typical of this species.

Only two specimens comparable to *E. plana* are available in the Winton assemblages. Their lanceolate leaf shape and tapering, pointed apices prevent certain allocation to that species. In these respects the Winton specimens are similar to *Elatocladus longifolium* Baldoni 1980 and *Podocarpus inopinatus* Florin 1940. However, both of these South American Mesozoic species are characterized by very small (<8mm long) leaves attached to long slender axes. The lack of finer morphological detail and fructifications on the Winton specimens prevents comparison with fertile or cuticle-based species such as *E.*

FIG. 14. Angiosperm sp. A. A-E, isolated leaves. A, QMF32579, x 1. B, QMF32451, x 1. C, QMF32448, x 1. D, QMF32452, x 1. E, QMF32449, x 1. F, enlarged detail of fig. 14E showing oblique venation and toothed margin, QMF32449, x 3. G, ?unexpanded leaf, QMF32631, x 10.

Family TAXODIACEAE

cf. *Austrosequoia wintonensis*
 Peters & Christophel, 1978
 (Figs 10B,D, 11A-I)

Athrotaxis australis Bose, 1955: 385; pl. 1, fig. 15; pl. 2, figs 16, 17, 24-25; text-fig. 1a.

Athrotaxis selligii Bose, 1955: 386; pl. 2, figs 18-25; text-figs 1b, 1c.

cf. *Austrosequoia wintonensis* Peters & Christophel, 1978: 3124, figs 2-7.

MATERIAL EXAMINED

L406: QMF32445, L717: QMF32490, QMF32491, QMF32495, QMF32504, QMF32507, QMF32509, QMF32519, QMF32521, QMF32526, QMF32529, QMF32530, QMF32536, QMF32546, QMF32550, QMF32571, QMF32605, QMF32608, QMF32609, QMF32611, QMF32612, QMF32614.

DESCRIPTION

Slender to thick (2-7mm wide) irregularly branched axes bearing helically arranged leaves (Fig. 11D-G). Older (larger) axes typically bearing tightly adpressed, short (<4mm wide, <4mm long) rhomboid scale-like leaves covering entire stem surface or in largest stems separated by <1mm grooves. Small axes bear short (<1mm wide, <2mm long), rhomboid, tightly adpressed, scale-like leaves covering entire stem surface or short (<1mm wide, <3mm long) spinose leaves adpressed to stem, arched away from axis at up to 90° (Fig. 11C), or arched away from axis but distally hooked (Fig. 11D,F). Leaf apices pointed acute becoming obtuse in older leaves. Leaves show broad basal attachment. Slender (ultimate) twigs sometimes attached to cones (Fig. 11B,G,I) reaching 8mm wide, 10mm long, comprising spirally arranged wedge-shaped or peltate scales reaching 4mm long, 2mm deep (Fig. 11A,G,H). Cones commonly open. Distal end of cone scales expanded, rhomboid in lateral view with a central, <0.5mm, depression (on petrifications) or raised tubercle (on impressions). A single spinose 8mm wide, 7mm long ovate organ (QMF32509) attached to a slender scale-bearing terminal twig may represent an under-developed ovulate cone of this species.

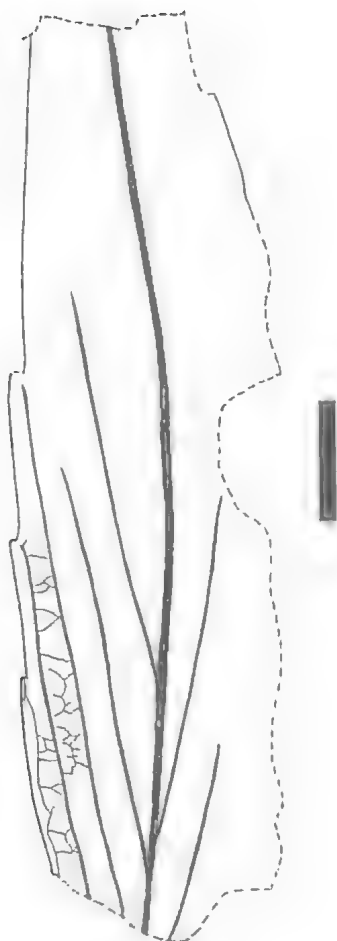
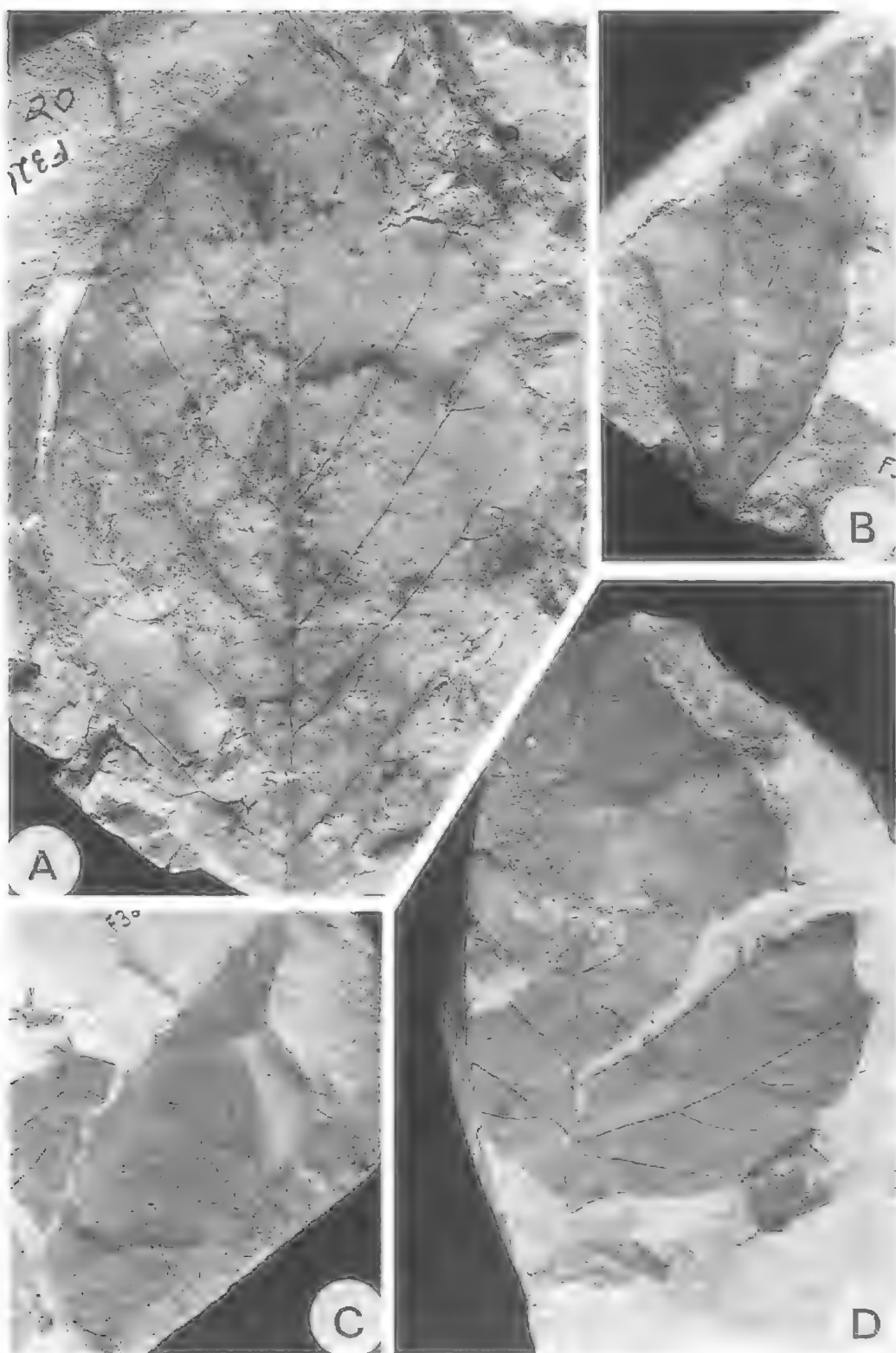


FIG. 15. Angiosperm sp. A, QMF32449, line drawing of specimen in Figs 14E,F showing details of venation. Scale bar: 5mm.

papillosa Baldoni 1980 and *Morenoa fertilis* Del Fueyo, Archangelsky & Taylor 1990. Dimorphic foliage is not evident on the Winton specimens comparable to that claimed for *Elatocladus longifolia* Borkar & Chiplonkar 1973 from the mid-Cretaceous of India.

overleaf on p.296

FIG. 16. Angiosperm sp. B, isolated leaves. A, QMF32459, x 1. B, QMF32453, x 1. C, QMF32458, x 1. D, QMF32455, x 1.



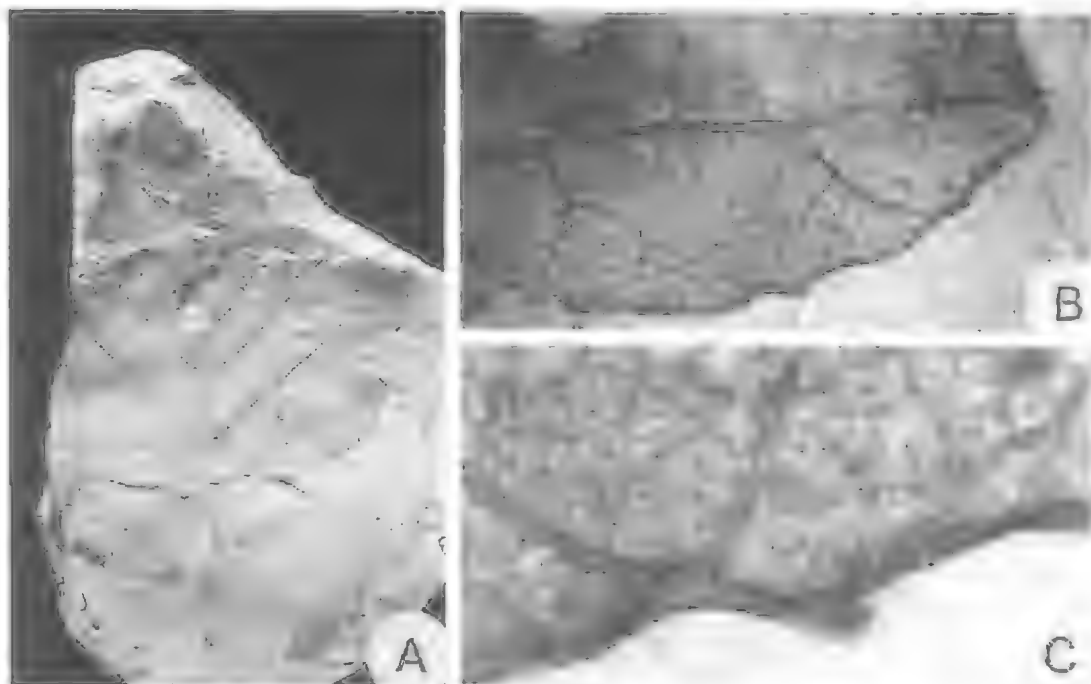


FIG. 17. Angiosperm sp. B, QMF32457. A, isolated leaf, $\times 0.8$. B, detail of leaf margin enlarged from Fig. 17A, $\times 4$. C, detail of leaf-margin tooth enlarged from Fig. 17B, $\times 15$.

COMPARISON AND REMARKS

The axis impressions, sometimes with attached cones, are morphologically identical to surface features evident on permineralized cones and foliage bearing axes assigned to *Austrosequoia wintonensis* by Peters & Christophel (1978). However, their conspecific nature can not be confirmed as *A. wintonensis* was defined largely upon anatomical features not available in the impressions. Cone impressions and casts assigned to *Athrotaxis selligii* by Bose (1955) appear to be identical to the Winton material. His foliage-bearing axes (*Athrotaxis australis* Bose) are also closely comparable to the Winton specimens although some leaves of *A. australis* appear to have more attenuated apices. We consider that *Athrotaxis australis*, *Athrotaxis selligii*, *Austrosequoia wintonensis*, and the impressions described here are probably conspecific but have previously been described as separate species owing to their differing fossilization states and incomplete preservation. Of these taxa *Athrotaxis australis* has nomenclatural priority, however, the anatomical studies of Peters & Christophel (1978) show that the ovulate cones have an architecture differing in several respects from extant *Athrotaxis* species. We propose the retention of *Austrosequoia wintonensis* for anatomically preserved remains but

place those specimens lacking cellular details under more open nomenclature.

Foliage and ovulate cones of *Sequoia novaezeelandiae* Ettingshausen 1891 from the Upper Cretaceous of New Zealand are possibly also conspecific with the Winton specimens. The New Zealand example possesses a short spine on the tip of the cone scales. This feature has not been detected on the Winton cone impressions although some of the permineralized cone scales of *Austrosequoia wintonensis* illustrated by Peters & Christophel (1978) show a low protuberance.

Broad, scale-like leaves on larger branches amongst the present material are comparable in shape to the rhomboidal, spirally inserted, imbricate leaves of the extant Tasmanian *Athrotaxis cupressoides* and the Early Tertiary Tasmanian *Athrotaxis ungeri* (Halle) Florin 1940. Slender terminal axes from the Winton Formation commonly also show short spinose leaves similar to *Athrotaxis selaginoides*, *Athrotaxis tasmanica* Hill, Jordan & Carpenter from Oligocene sediments of Tasmania is distinguished by the prominent abaxial keels on its leaves (Hill et al., 1993). The spinose leaves within the range of foliage attributed to cf. *Austrosequoia wintonensis* also fall close to the dimensions of some leaves referred herein to "Conifer indet." although the

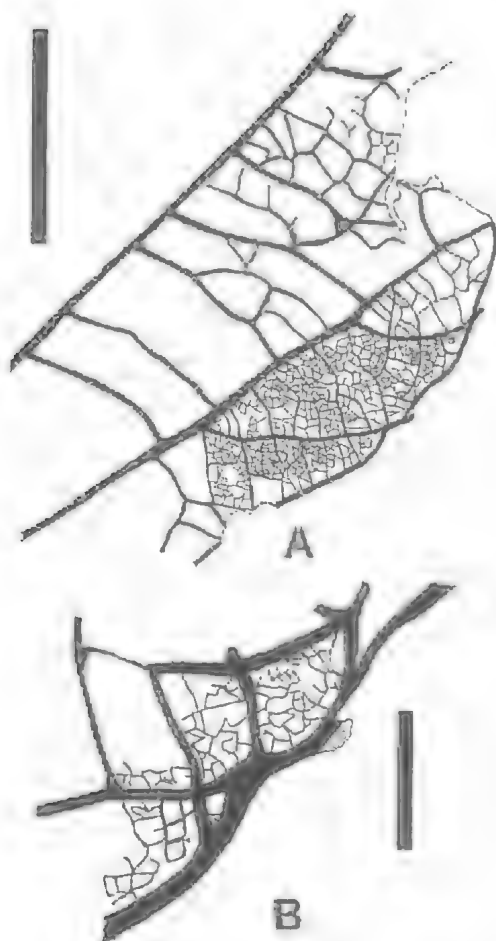


FIG. 18. Angiosperm sp. B, QMF32457. A, line drawing showing venation detail from Fig. 17B. B, line drawing showing venation detail from Fig. 17C. Scale bars: A = 10mm, B = 2mm.

latter are typically flattened and are not distally hooked.

Family UNCERTAIN

Conifer sp. A (Figs 10C, 12A-D)

MATERIAL EXAMINED

L406: QMF32615, NMVP199579. L717: QMF32481, QMF32497, QMF32522, QMF32531,

QMF32547, QMF32552, QMF32564, QMF32604, QMF32610, QMF32616, QMF32617.

DESCRIPTION

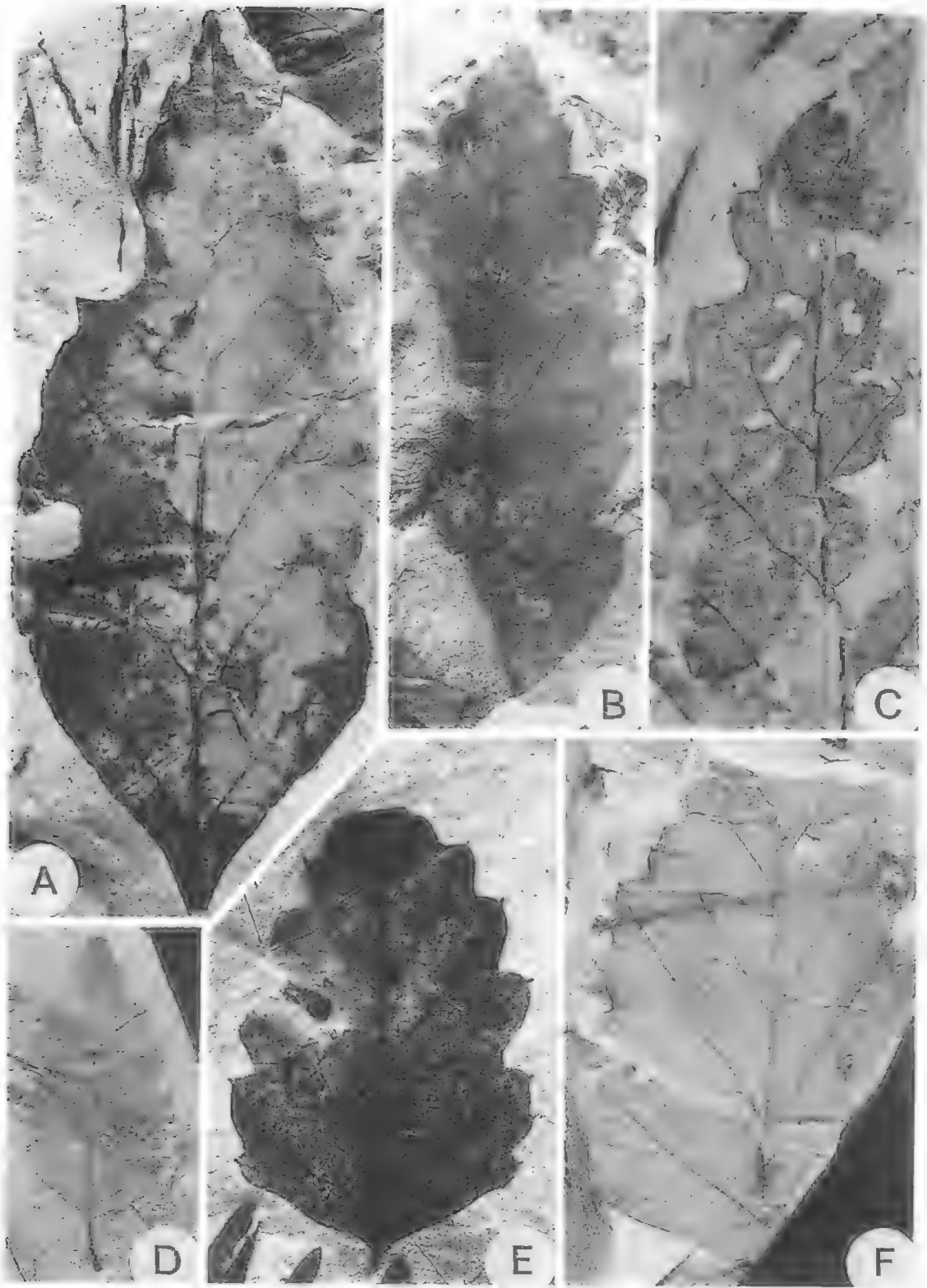
Slender (<2mm wide) axes bearing variable spirally inserted leaves. Shoots <4.2cm long, mostly detached, rarely branched irregularly. Leaves range from diminutive (<0.5mm wide, <1.5mm long) scale-like appendages adpressed against the axis (Figs 10C, 12C) to linear (<1mm wide, 12mm long) needles strongly arched away from the axis (Fig. 12A-D). Leaf base slightly clasping?, twisted to align leaves in a common plane (Fig. 12C). Longer leaves commonly arched sharply <2mm above base then gently flexed distally, remaining straight, or gently reflexed (up to 70° to axis) along outer part of lamina (Fig. 12A). Fructifications unknown.

COMPARISON AND REMARKS

This conifer species shows a broad range of foliage types some of which are morphologically similar to certain examples of cf. *Elatocladus plana* and cf. *Austrosequoia wintonensis* occurring at the same locality. However, Conifer sp. A is distinguished by its slender (needle-like) leaves which are strongly arched (but not contracted) near the base to align the leaves in two ranks. Several extant conifer genera produce superficially similar foliage. The lack of cuticular details and fructifications inhibits confident attribution of these remains to any genus. A possible affinity with the Taxales is suggested by their slender, slightly flattened, needle-like, univeined, seasonally variable, two-ranked leaves which appear to have been consistently shed while still attached to the terminal twigs.

Conifer sp. A is most similar to *Podocarpus hochstetteri* Ettingshausen 1891 from the New Zealand Upper Cretaceous which has similar straight or falcate leaves which are strongly arched at the base. Better material from the *P. hochstetteri* type locality is required for more detailed comparison. The Winton specimens are also closely comparable to several foliage-bearing twigs variously assigned to *Elatocladus confertus* or *Elatocladus plana* from the Australian Jurassic and Cretaceous (Walkom, 1919a, 1928; Hill et al., 1966).

FIG. 19. Angiosperm sp. C, isolated leaves. A, QMF32489, x 1.6. B, QMF32557, x 1.75. C, QMF32554, x 1.8. D, QMF32559, x 1.5. E, QMF32562, x 1.5. F, QMF32517, x 1.5.



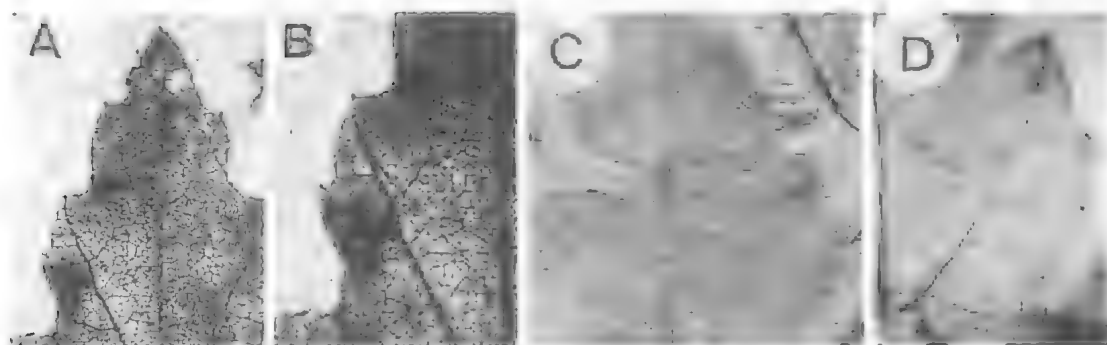


FIG. 20. Angiosperm sp. C. A, QMF32524, isolated leaf, $\times 2$. B, QMF32524, detail of leaf margin enlarged from Fig. 20A, $\times 3.2$. C, QMF32512, isolated leaf, $\times 1.5$. D, QMF32512, detail of leaf margin enlarged from Fig. 20C, $\times 2$.

Incertae sedis
Order PENTOXYLALES
Family PENTOXYLACEAE

Taeniopteris Brongniart, 1828
Taeniopteris sp.
(Fig. 13)

MATERIAL EXAMINED

L406: NMVP199580, NMVP199581.

DESCRIPTION

?Spathulate entire or slightly undulate-margined leaves, apex and base absent from both specimens. Leaves reaching in excess of 70mm long and 22mm wide. Arrangement on axis uncertain. Stout midrib reaching 2mm wide near base, tapering slightly towards apex. Lateral veins depart midrib at 60° - 70° and pass straight to the margin without branching or with one, rarely two, dichotomies. No marginal vein present. Vein concentration 23-28 per cm along margin. Fructifications and cuticular details unavailable.

COMPARISON AND REMARKS

Although these leaves are not associated with fructifications they are morphologically similar to taeniopterid leaves from Early and mid-Cretaceous strata elsewhere in Australia and are here regarded as most probably pentoxylalean. Similar leaves are produced by some ferns (e.g., *Asplenium*) hence a pteridophytic affinity can not be entirely excluded.

The few specimens and incomplete preservation of the available material prevents detailed comparison with other species. However, *Taeniopteris* sp. differs from the widespread Australasian Early Cretaceous *T. daintreei* McCoy

1874 and the morphologically similar Indian *T. spatulata* Oldham & Morris 1863 by the lesser angle of departure of the secondary veins from the midrib. *Taeniopteris elongata* Walkom 1918 from the Maryborough Formation (Aptian) also has secondary veins oriented at around 90° to the midrib and may be synonymous with *T. daintreei*. *Taeniopteris howardensis* Walkom 1919 from the Burrum Coal Measures (Albian), Maryborough Basin, is morphologically closest to *Taeniopteris* sp. in having secondary veins at around 70° to the midrib although the venation density in the former is reportedly much greater. *Taeniopteris stipulata* Hector 1886 from the Late Cretaceous of New Zealand (McQueen, 1956) is also closely comparable in its venation orientation although it appears to be represented by narrow elliptical or lanceolate leaves.

Division MAGNOLIOPHYTA
Class MAGNOLIOPSIDA
Subclass UNCERTAIN

Angiosperm sp. A
(Figs 14A-G, 15)

MATERIAL EXAMINED

L406: QMF32448, QMF32449, QMF32451, QMF32452, QMF32579. L552: QMF32631.

DESCRIPTION

Leaves; lamina up to 125mm long and 12mm wide, linear, with a cuneate base and a long, attenuate apex, petioles not preserved. Margin serrate, each tooth terminating a secondary vein. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight or slightly curved; secondary veins closely spaced,

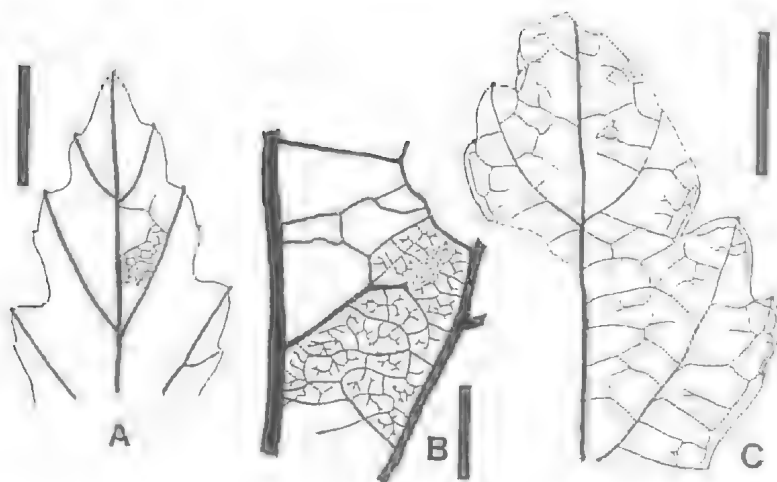


FIG. 21. Angiosperm sp. C. A, QMF32524, line drawing of specimen in Fig. 20A. B, QMF32524, detail of venation enlarged from Fig. 21A. C, QMF32512, line drawing showing detail of venation of specimen in Fig. 20C. Scale bars: A, C = 10 mm, B = 2 mm.

arising from midvein at 30° angle; tertiary veins linking secondary veins, but indistinct.

COMPARISON AND REMARKS

A single specimen has the complete lamina preserved and shows the base and apex shape (Fig. 14A). It has a lamina 100mm long, which extends another 25mm as a long, narrow, attenuate apex. The other five specimens are fragmentary, but exhibit the acute secondary veins terminating in widely-spaced, distally pointing, serrations along the otherwise entire leaf margin (Fig. 14B-G). A reticulate network of tertiary veins toward the margin is just evident in one specimen (Figs. 14F, 15), but otherwise higher order venation is unclear. One very small, possibly not fully expanded, leaf from L552 shows the leaf margin's teeth well developed but no secondary or higher order venation (Fig. 14G).

Subclass HAMAMELIDAE
Order ?FAGALES
Family UNCERTAIN

Angiosperm sp. B
(Figs 16A-D, 17A-C, 18A,B)

MATERIAL EXAMINED

L406: QMF32453-60, QMF32577. L717: QMF32556, QMF32583. L552: QMF32468-71. Conway's Claim: ?QMF17458.

DESCRIPTION

Leaves; lamina up to 145mm long and 70mm wide, ovate to elliptical, with asymmetrical cuneate base and acuminate tip; petioles reaching 36mm long. Margins entire to gently lobed or slightly serrate about secondary vein endings, which are terminated by a short setaceous tooth. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight; secondary veins 14 to 16, paired basally, diverging at 50° , upper veins sometimes more acute than lower veins; prominent tertiary veins oriented obliquely with respect to midvein, linking secondary veins; quaternary and higher order veins forming irregular polygonal areoles

with branched veinlets. Secondary veins with exmedial branches that become continuous distally to form a distinct fimbrial vein along the leaf margin.

COMPARISON AND REMARKS

The twelve specimens listed above show minor variation in leaf shape and venation. Several specimens are elliptical with entire margins and uniformly diverging secondary veins (Fig. 16A,B). Several other leaves are relatively broader, tend to be ovate, have slightly lobed margins, and have their more proximal secondary veins diverging from the midvein at a less acute angle than those distally (Figs 16D, 17A). The narrower specimens tend to have a more cuneate base, but in all specimens where the base of the lamina is preserved it is distinctly asymmetrical. All specimens have identical higher order venation, and have the exmedial secondary vein branches continuous as a marginal fimbrial vein that supplies a short, setaceous tooth at the point where each secondary vein or one of its branches reaches the leaf margin (Figs 17A-C, 18A,B).

These leaves are similar in size and venation to several taxa Pole (1992) described from Cenomanian localities of the Matakaea Group, New Zealand (parataxa MATA-1 Pole 1992: figs 2, 3, and MATA-2 Pole 1992: fig. 4). All are relatively large hamamelid leaves with simple

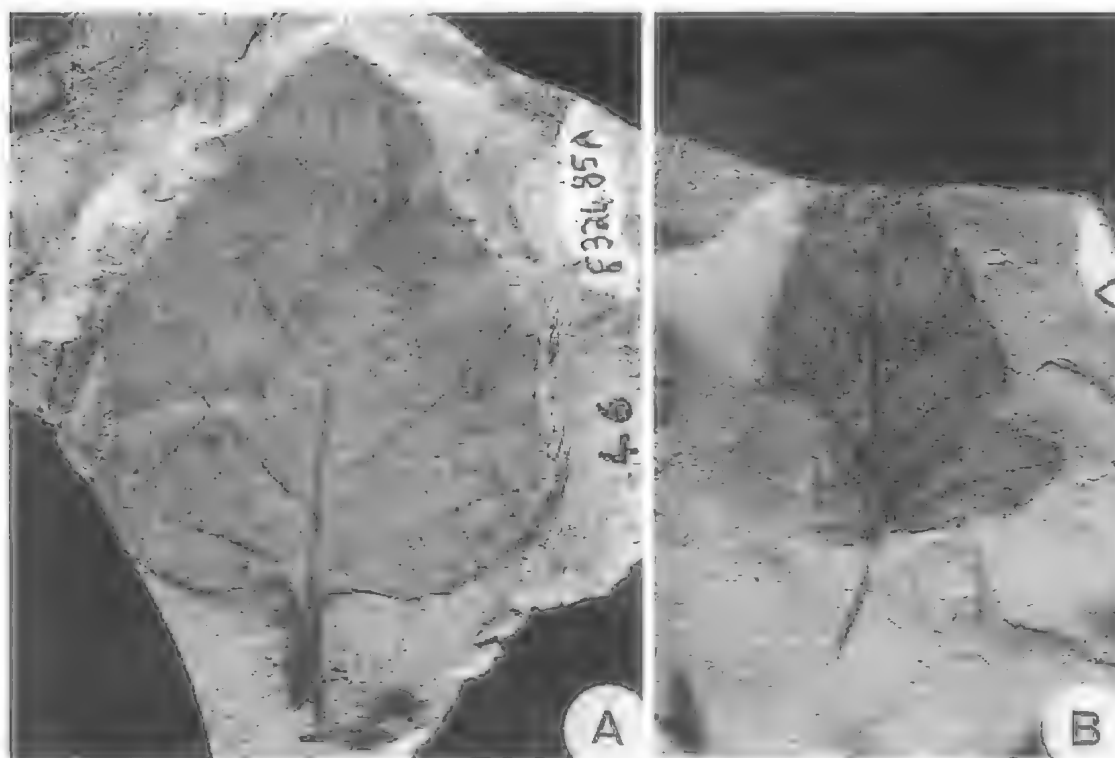


FIG. 22. Angiosperm sp. D, isolated leaves. A, QMF32485, $\times 1.4$; B, QMF32487, $\times 1.5$.

craspedodromous venation and prominent, obliquely oriented, tertiary veins.

Angiosperm sp. C
(Figs 19A-F, 20A-D, 21A-C)

MATERIAL EXAMINED

L717a: QMF32483, QMF32486, QMF32489, QMF32506, QMF32508, QMF32510-12, QMF32517, QMF32523, QMF32524, QMF32539, QMF32554, QMF32557, QMF32559, QMF32562, QMF32565, QMF32566, QMF32568-70, QMF32573, QMF32581, QMF32582, QMF32584-91.

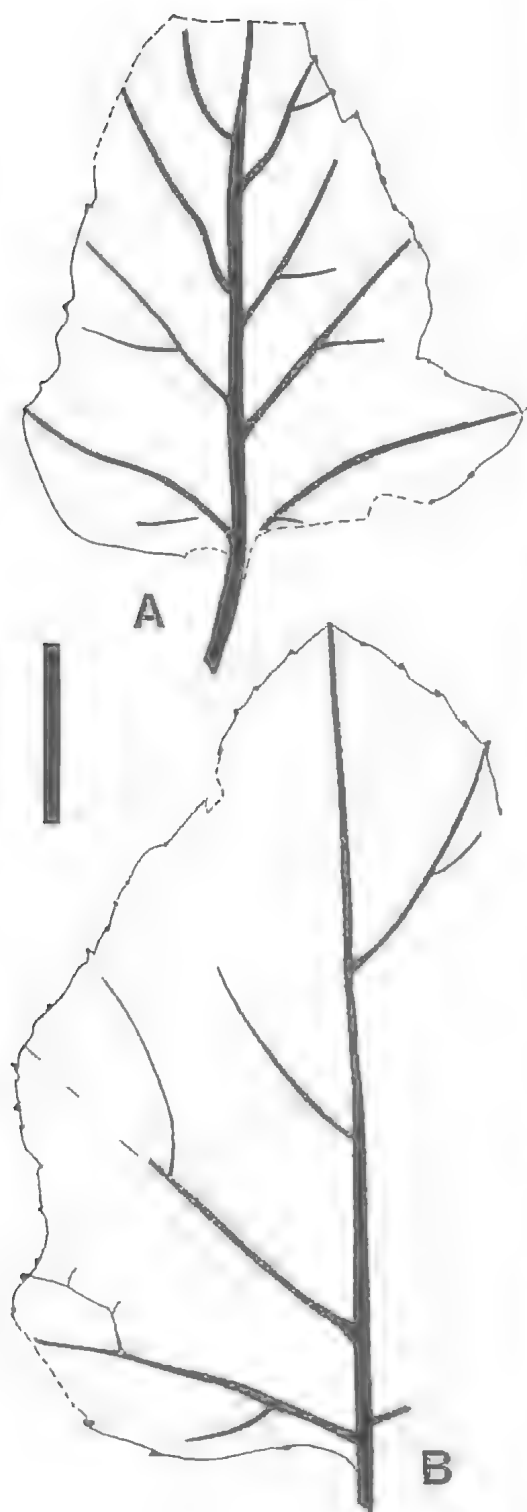
DESCRIPTION

Leaves; lamina up to 95mm long and 46mm wide, ovate to elliptical, with obtuse to cuneate base and acute to slightly mucronate apex, petioles preserved up to 6mm long. Margins lobed about secondary veins, which terminate in a mucronate tooth; smaller leaves are mucronate only at secondary vein endings, larger leaves have exmedial secondary vein branches terminating serrulations. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight; secondary veins 10-14, paired basally,

diverging from midvein at $35-60^\circ$, upper veins more acute than lower veins; tertiary veins randomly oriented; higher order veins forming a random reticulate network of areoles with twice branched veinlets.

COMPARISON AND REMARKS

This is the most numerous Winton angiosperm leaf type, with approximately 20 specimens examined from L717. They are superficially similar to Angiosperm sp. B from L406 in their general shape and simple craspedodromous venation, but they are generally much smaller and differ in several other respects. Their margins are more deeply lobed, and the secondary veins and their branches do not form a prominent fimbrial vein (Figs 20A-D, 21C). Tertiary veins are not as prominent as those of Angiosperm sp. B, and they are randomly oriented rather than consistently oblique to the midvein. Higher order veins form a network of areoles with branched veinlets (Fig. 21A,B). Leaf margins are relatively deeply lobed, each lobe with a mucronate tooth at its apex, which terminates a secondary vein; in larger leaves, exmedial secondary vein branches may also supply a toothed lobe, especially in the prox-



imal portion of the leaf. The sinus between each lobe is gently rounded. The midvein extends to the apex of the leaf, and also terminates in a mucronate tooth. Morphological variation is similar to that seen in *Angiosperm* sp. B and extant hamamelids; some leaves are elliptical (Fig. 19A,B), others ovate (Fig. 19E,F). The more ovate leaves tend to have a decreasing secondary vein divergence angle from base to apex, and more strongly developed secondary vein branched proximally (Fig. 19E,F). In some leaves, only the basal pair of secondary veins are opposite, in others up to four pairs are oppositely arranged in the proximal half of the leaf. Only one small leaf has the petiole preserved intact; it is 6mm long and the lamina is 29mm long (Fig. 19D).

These leaves are reminiscent of *Nothofagus praequercifolia* (Ett.) Pole recorded from Santonian to early Maastrichtian localities in the Taratu Formation, New Zealand (Pole, 1992). Features in common are the lobed leaf margin with mucronate tips, and simple craspedodromous venation with irregularly oriented tertiary veins (see Pole, 1992: figs. 23-31). Several incomplete Winton specimens may have had more deeply dissected margins, resembling *Nothofagus melanoides* Pole, also from the Taratu Formation.

Angiosperm sp. D
(Figs 22A,B, 23A,B)

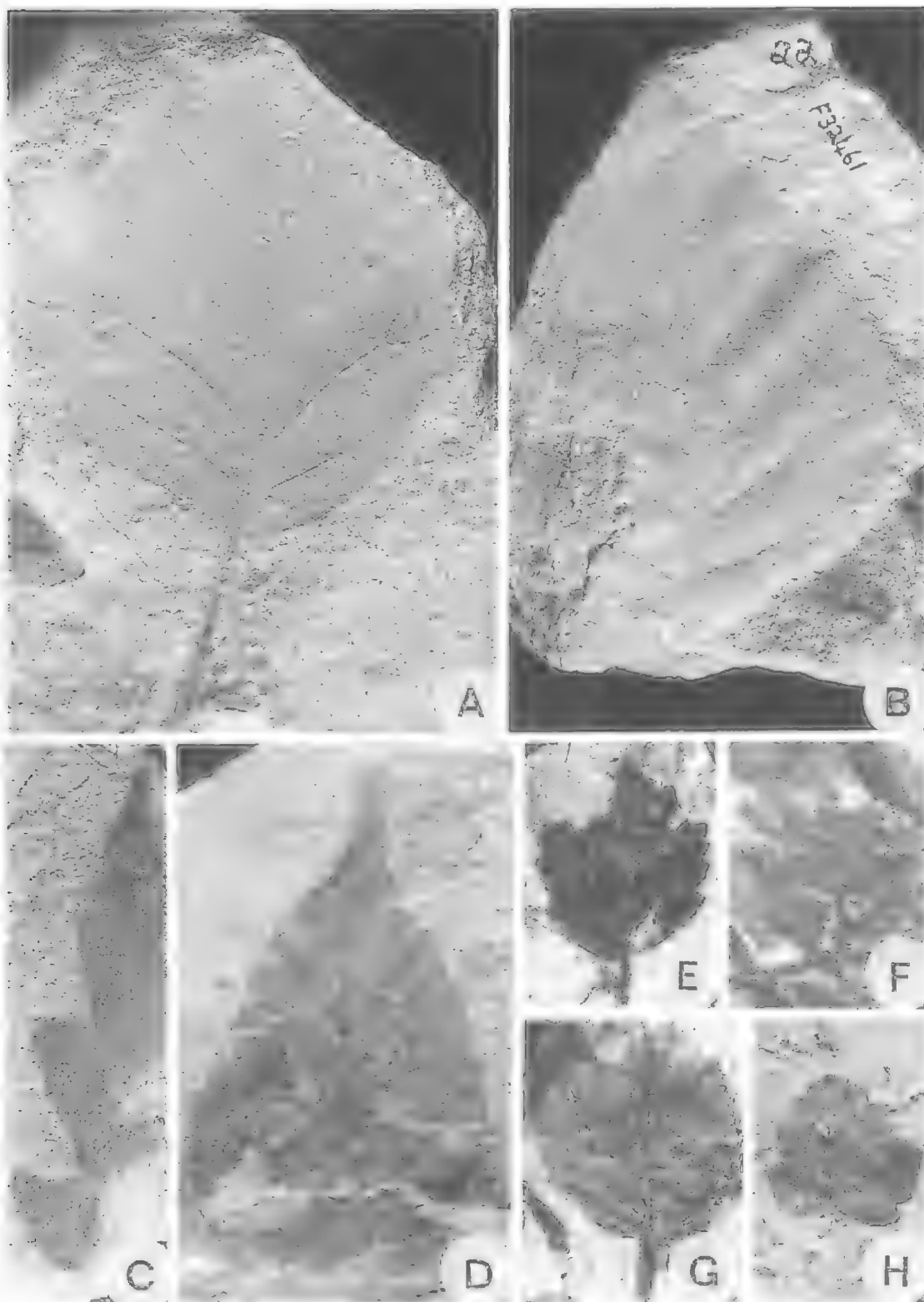
MATERIAL EXAMINED

L717: QMF32485, QMF32487.

DESCRIPTION

Leaves; lamina up to 52mm long and 45mm wide, ovate, with an obtuse base and obtuse apex with mucronate tip, petiole 10-12mm long. Margins slightly lobed about secondary veins, and serrulate with mucronate teeth terminating secondary veins and their exmedial and occasional admedial branches. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight; secondary veins 10, paired basally, diverging from midvein at 45-50°, upper veins more acute than lower veins; higher order venation not preserved.

FIG. 23. *Angiosperm* sp. D, line drawings of isolated leaves. A, QMF32487. B, QMF32485. Scale bar: 10mm.



COMPARISON AND REMARKS

Only two specimens of this leaf type were identified. They are distinguishable from *Angiosperm* sp. C, from the same locality, by their gently lobed rather than dissected outline and their almost deltoid shape. One specimen has such strongly developed basal segments it is almost trilobed (Figs 22B, 23A). The margin is serrate, each serration having a dark, glandular appearance. Some of these serrations clearly terminate a secondary vein or exmedial secondary vein branch, and the others probably also terminate a secondary vein or its branches. There is no evidence of a marginal, fimbrial vein.

Angiosperm sp. E
(Fig. 24A,B)

MATERIAL EXAMINED

L224: QMF32461-3.
L165: QMF32464, QMF32593.

DESCRIPTION

Leaves; lamina up to 80mm long and 60mm wide, ovate, with asymmetrical base, apex not preserved. Primary venation pinnate, secondary venation simple craspedodromus; midvein curved; secondary veins 12-16, diverging from midvein at 45-60°, paired proximally; tertiary venation prominent, oblique to midvein; higher order venation not preserved. Margins more or less entire.

COMPARISON AND REMARKS

Three specimens of this leaf type are preserved from L224. They are poorly preserved in a coarse, white, sandy matrix, and do not show the same fine detail as specimens from other Winton locations, making comparison difficult. They most closely resemble the more ovate specimens of *Angiosperm* sp. B from L406 having similar size, asymmetrical base, and prominent, oblique, tertiary venation, and may be conspecific with those leaves. The main differences are that two specimens have a curved midvein (although this may be taphonomic deformation, Fig. 24A,B), and two of the three leaves have some secondary veins that dichotomize rather than produce exmedial branches. The coarse nature of the sedi-

ment precludes assessment of the presence or absence of a fimbrial vein.

Angiosperm sp. F
(Fig. 24C)

MATERIAL EXAMINED

L406: QMF32450.

DESCRIPTION

Leaf; lamina greater than 65mm long, 50mm wide, prominent midvein, margin deeply cleft.

COMPARISON AND REMARKS

Only one specimen is known from L406. It is poorly preserved, the venation pattern is not evident, and the specimen shows no details other than gross outline of the margin. It looks superficially like the most dissected leaves of *Angiosperm* sp. C from L717, but little else can be said of its affinities.

Angiosperm sp. G
(Fig. 24D)

MATERIAL EXAMINED

?L717 Dalkeith: QMF18106.

DESCRIPTION

Leaf; lamina greater than 75mm long, 45mm wide, ovate, attenuate apex, base not preserved. Margins cleft about secondary veins and their exmedial branches, each tooth terminated by a mucronate tip. Primary venation pinnate, secondary venation simple craspedodromus; midvein straight or slightly curved; secondary veins c. 10, paired in proximal portion of leaf, diverging from midvein at 20-30°, higher order venation not preserved.

COMPARISON AND REMARKS

This leaf type is represented by a single specimen (Fig. 24D). It is distinguished from other Winton angiosperms by its attenuate apex, serrate margin that is more or less equally cleft between the secondary veins and exmedial secondary vein branches, and acutely angled sinuses between serrations. Pole (1992: fig 40) illustrated a similar leaf (parataxon TARA-18) from the early

previous page

FIG. 24. A, B, *Angiosperm* sp. E, isolated leaves. A, QMF32462, x 1. B, QMF32461, x 1. C, *Angiosperm* sp. F, QMF32450, leaf fragment, x 1. D, *Angiosperm* sp. G, QMF18106, isolated leaf, x 1. E-H, *Angiosperm* sp. 11, isolated leaves. E, QMF32474, x 1.9. F, QMF32472, x 1.8. G, QMF32473, x 2. H, QMF32475, x 2.

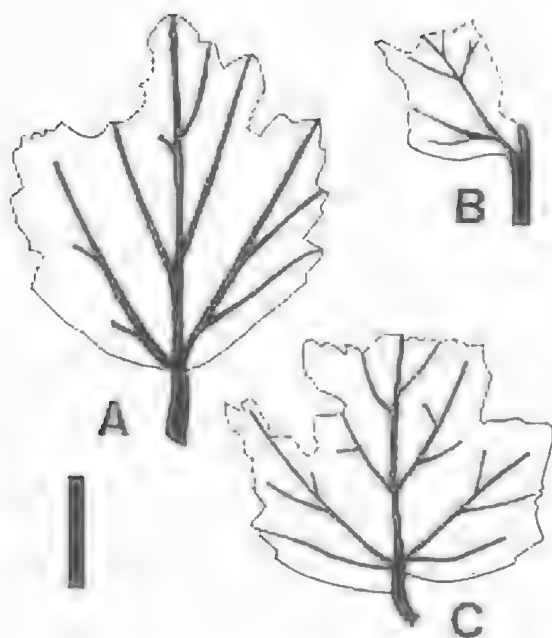


FIG. 25. *Angiosperm* sp. H, line drawings of isolated leaves. A, QMF32474. B, QMF32632. C, QMF32472. Scale bar: 5mm.

Maastrichtian of the Taratu Formation, New Zealand, which he tentatively assigned to *Betulaceae*.

***Angiosperm* sp. H**
(Figs 24E-H, 25A-C)

MATERIAL EXAMINED

L552: QMF32472-5, QMF32592, QMF32632.

DESCRIPTION

Leaves; lamina up to 20mm long and 20mm wide, ovate, with cordate to obtuse base and obtuse apex, petiole preserved up to 3mm. Venation simple craspedodromous; midvein straight; secondary veins c.8, diverging from midvein at 45-60°, paired basally; higher order venation not preserved. Margins incised, more deeply cleft about main secondary veins than secondary vein branches.

COMPARISON AND REMARKS

These are the smallest of the Winton angiosperm leaves. Only a few specimens are complete, but there are numerous lamina fragments in matrix from L552. The largest complete leaf has a lamina 20mm long, but a few of the dispersed lamina fragments suggest some leaves were slightly larger. There is some possibility that they are unexpanded leaves of

one of the previously described taxa, possibly *Angiosperm* sp. B, which also occurs at the same locality. The veins and lamina have the appearance of being relatively thick, and some fragments look to belong to leaves attached to the same shoot. There are numerous twigs associated with the leaves, and the dense accumulation of leaves and lamina fragments in the matrix may derive from a single branch.

**WINTON ASSEMBLAGES IN RELATION
TO OTHER CRETACEOUS FLORAS**

The Winton Formation assemblages differ slightly in their taxonomic composition (Table 1) and their stratigraphic relationships to one another are uncertain. However, the presence of some shared taxa between localities suggests that the assemblages are more or less coeval. The fossils, varying from delicate fern fronds to robust conifer branches, and including a series of ginkgophyte, pentoxylalean, and angiosperm leaf types, suggest that the assemblages were derived from diverse plant communities of herbaceous and woody plants. The relatively complete preservation of several leaf types suggests an absence of turbulent transport to their site of deposition and implies that most if not all the remains were derived from very local sources. The Winton Formation suites, therefore, show the earliest Australian macrofossil representation of a vegetation type comprising abundant and diverse angiosperms mixed with typical Mesozoic fern and gymnosperm elements (Fig. 26).

The earliest unequivocal evidence of flowering plants are monosulcate pollen grains from the Hauterivian (middle Early Cretaceous) of Israel (Brenner, 1984) and southern England (Hughes & McDougall, 1987). Monosulcate or monosulcate-derived pollen is characteristic of extant magnoliid dicotyledons and monocotyledons. Triaperturate pollen diagnostic of the non-magnoliid ("higher") dicotyledons appears slightly later at around the Barremian-Aptian boundary. A subsequent major diversification of angiosperms through the mid-Cretaceous is clearly established from analyses of both megaflores and palynoflores (Hickey & Doyle, 1977; Lidgard & Crane, 1988, 1990; Crane & Lidgard, 1989, 1990). In the Northern Hemisphere angiosperm pollen first appears and becomes both abundant and diverse at low palaeolatitudes, and only subsequently becomes important in middle and high palaeolatitudes (Hickey & Doyle, 1977; Crane & Lidgard, 1989). There are less data for the South-

TABLE 1. Distribution of fossil plant taxa at Eromanga Basin localities.

| Species | L406 | L717 | L552 | L224 | L165 | Conway's Claim |
|---|------|------|------|------|------|----------------|
| <i>Phyllopteroides macclymontae</i> | | + | | | | |
| <i>Microphylopteris</i> sp. cf. <i>M. gleichenoides</i> | | | + | | | |
| <i>Cladophlebis</i> sp. | | + | + | | | |
| <i>Sphenopteris</i> sp. cf. <i>S. warragulensis</i> | | | + | | | |
| <i>Sphenopteris</i> sp. | | + | | | | |
| indeterminate fern pinnule | | + | | | | |
| <i>Taeniopteris</i> sp. | + | | | | | |
| <i>Ginkgo wintonensis</i> | | + | | | | |
| <i>Araucaria</i> sp. cf. <i>A. mesozoica</i> | + | + | | | | |
| Araucarian microsporangiate cones | + | + | | | | |
| Araucarian ovulate cone scales | + | + | | | | |
| <i>Elatocladus</i> sp. cf. <i>E. plana</i> | | + | | | | |
| cf. <i>Austrosequoia wintonensis</i> | + | + | ? | | | |
| Conifer sp. A | + | + | | | | |
| Angiosperm sp. A | + | | + | | | |
| Angiosperm sp. B | + | + | + | | | ? |
| Angiosperm sp. C | | + | | | | |
| Angiosperm sp. D | | + | | | | |
| Angiosperm sp. E | | | | + | + | |
| Angiosperm sp. F | + | | | | | |
| Angiosperm sp. G | | + | | | | |
| Angiosperm sp. H | | | + | | | |

ern Hemisphere, but it appears that the same latitudinally diachronous pattern occurs (Drinnan & Crane, 1989). There is good evidence for considerable diversity in the Magnoliidae by the end of the Early Cretaceous, but quantitative analysis of Cretaceous palynofloras indicates that the mid-Cretaceous floristic transition to angiosperm-dominated floras mainly reflects the increasing diversity of non-magnoliid dicotyledons (Crane & Lidgard, 1989). These patterns imply that the transition from a pre-Cretaceous fern/gymnosperm vegetation to a flora dominated by angiosperms at the end of the Cretaceous has two components. The first is the "initial appearance" evidenced by monosulcate pollen representing the magnoliid dicot/monocot grade. The second component is "floristic domination" largely resulting from the diversification of triaperturate pollen diagnostic of the non-magnoliid dicot clade.

The Winton Formation is stratigraphically and floristically associated with the second component, the increasing diversity and dominance of non-magnoliid dicotyledons. All but one of the

angiosperm leaf taxa are of the simple hamamelid type, with probable fagaceous or betulaceous affinity. All have simple craspedodromous venation and, where higher order venation is preserved, it forms a well developed reticulum. The composition of the Winton angiosperm flora is very different to the well documented middle Cretaceous angiosperm floras of the Potomac Group on the Atlantic Coastal Plain of the United States, which form the basis of current hypotheses of angiosperm origin and diversification (Doyle & Hickey, 1976; Hickey & Doyle, 1977). The Winton flora does not contain any magnoliid leaves. Small "palaeoherb" leaves with unordered venation are characteristic of Potomac Group Zone I (Aptian) localities, peltate nelumbaceous types are common in the Albian Subzone II-B,

and elliptical leaves of magnoliaceous/lauraceous affinity are prominent in the upper half of the Potomac sequence. The hamamelid component of the Potomac Group flora dominates Subzones II-B and III (Albian-Cenomanian) and consists largely of trilobed, palmately veined (*Araliopsoides*) and compound, pinnate (*Sapindopsis*) leaves that are of platanaceous and rosiid affinities (Crane et al., 1993; Upchurch et al., 1994).

Pole (1992) described a diverse collection of angiosperm leaves from several New Zealand localities ranging in age from Cenomanian to Maastrichtian. The hamamelid components are very like the leaves from the Winton Formation, but the New Zealand floras contain several extra forms, notably actinodromous, *Cinnamomum*-like, lauraceous leaves, several taxa with brochidodromous venation showing prominent secondary loops, and palmately veined leaves with prominent suprabasal secondaries. Daniel et al. (1990) summarised a New Zealand Cenomanian flora from the Clarence Series as having a range of magnoliid and hamamelid angiosperm

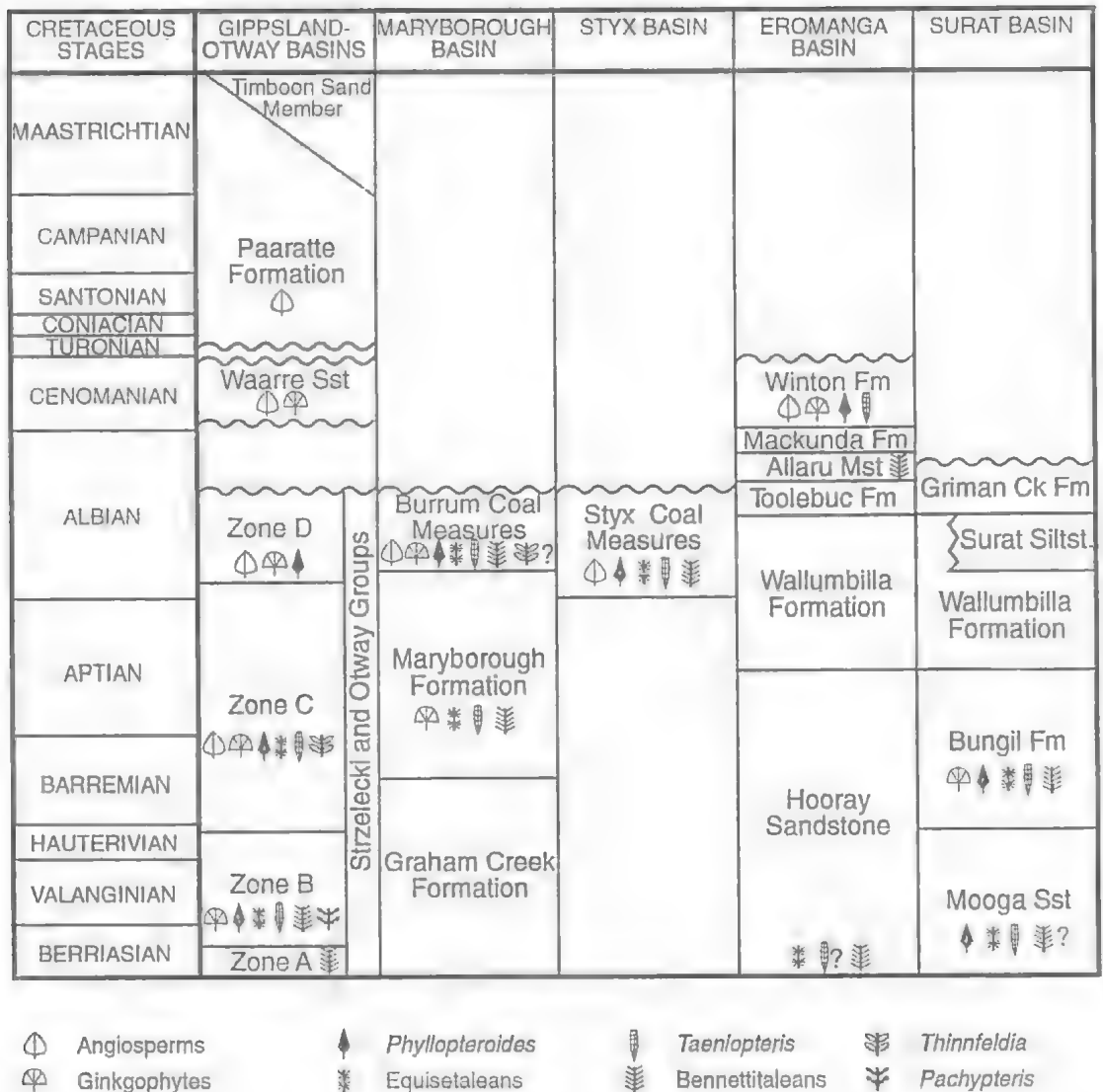


FIG. 26. Stratigraphic correlation of various Australian Cretaceous plant-bearing formations showing the distribution of selected plant groups.

leaves associated with a more typical Cretaceous conifer-“pteridosperm” assemblage including araucarians, several genera of Bennettitales, *Thinnfeldia*, Pentoxylales (*Taeniopteris*), cycads and *Ginkgo*; of these Bennettitales and *Thinnfeldia* are completely absent from the Winton gymnosperm assemblage, which consists predominantly of conifers.

Angiosperm leaves have been recorded from other mid-Cretaceous strata in eastern Australia (Fig. 26). Walkom (1919a) provided line draw-

ings of several pinnately veined leaves from the Albian Burrum and Styx Coal Measures, central Queensland. These floras contain a number of non-angiosperm taxa that are morphologically similar to Winton elements, including *Cladophlebis*, *Phyllopteroides*, *Sphenopteris*, *Microphylopteris*, *Podozamites*, and especially *Ginkgo* and *Taeniopteris*. Bennettitales, which are absent in the Winton suites, are present in the Burrum and Styx floras. Medwell (1954b) illustrated two angiosperm leaves from an Albian

(latest Zone D) locality at Killara Bluff, western Victoria, and Douglas (1969) recorded a leaf and dispersed cuticle from similarly aged strata in subsurface drill core section (Yangery no. 1 bore). Zone D floras are well sampled from Victoria, and are dominated by *Elatocladus*, *Podozamites* and *Brachyphyllum* conifers, *Phyllopteroides*, and several finely dissected ferns. Bennettitales and *Taeniopteris* are absent, and *Ginkgo* is extremely uncommon. The Victorian Zone D floristic elements are not particularly like the similarly aged Burrum and Styx floras. The slightly younger Waarre Formation, which is known only from bore cores in western Victoria has yielded several small angiosperm leaves, and a species of *Ginkgo* similar to leaves found in the Winton, Burrum and Styx assemblages (Douglas, 1965).

Although the Winton Formation is known from only a small collection of localized floras, comparison with other floras of similar age provides an opportunity to propose a possible scenario of floristic transition through the Australian mid-Cretaceous. Valanginian to Aptian floras of southern Queensland and Victoria (Fig. 26) are essentially similar, and characterized by a predominance of conifers and linear *Taeniopteris* leaves with secondary veins perpendicular to the midvein. Together with a range of ferns such as *Cladophlebis* and *Sphenopteris*, they constitute an assemblage very similar to Jurassic strata of the Walloon Coal Measures (cf. Gould, 1974; McLoughlin & Drinnan, 1995); this is particularly evidenced by the perpetuation of early Mesozoic taxa such as *Palissya* cones in the Neocomian and Aptian of Victoria (Parris et al., 1995). Small leaved Bennettitales such as *Ptilophyllum* and *Otozamites* are a prominent component of earliest Cretaceous floras that persist through the Albian in the Burrum and Styx Coal Measures in Queensland, but have already largely disappeared from Victorian floras by the Barremian. Bennettitales have not been recorded from the well collected Zones C and D of Victoria. The youngest Australian bennettitaleans appear to be represented in the late Albian Allaru Mudstone of central Queensland (Rozefelds, 1986). The apparent absence of Bennettitales in the Winton flora suggests that they have entirely disappeared from eastern Australia by the Cenomanian. This is somewhat different to New Zealand, where a considerable diversity is reported for the Clarence Series (Daniel et al., 1990) and they remain a component of some floras until as late as the early Senonian (McQueen, 1956).

Taeniopterid leaves also disappear earlier from Victorian floras. Linear leaves of the *Taeniopteris daintreei* type are a common and distinctive index fossil for the Victorian Zone C (Barremian-Aptian), but the Zone D (Albian) and younger sediments are devoid of taeniopterid leaves. Broader *Taeniopteris* leaves with angled secondary venation are present in Burrum and Styx floras, and persist in the Winton flora. Ginkgophytes have a disrupted record. In Victoria, deeply dissected leaves of *Ginkgo australis* are a common component of Zone C floras, but they are absent from adjacent Zones B and D. Smaller, more compact, and less dissected *Ginkgo* leaves persist in the Zone D and Waarre Formation floras (Douglas, 1965, 1970), and are more reminiscent of specimens from Burrum, Styx and Winton. Although the data is very sparse, they suggest that a widespread and comparatively uniform, eastern Australian, earliest Cretaceous flora (e.g., Maryborough Formation of Queensland and Zone C of Victoria) differentiated into different Albian floras in Victoria (Zone D) and Queensland (Burrum/Styx), and that it was these latter, central-eastern, Burrum/Styx type, floras that influenced Cenomanian floras of the Winton Formation in Queensland and possibly the Waarre Formation in Victoria.

The decline of bennettitaleans, pentoxyleans, *Thinnfeldia*, *Pachypteris*, ginkgoaleans, and equisetaleans in the Australian flora appears to have occurred gradually through the Cretaceous and was matched by the appearance and steady increase in the diversity and abundance of angiosperms (Fig. 26). Eastern Australia remained in relatively high latitudes during the Cretaceous (Veevers et al., 1991) and although sea-levels varied considerably during that period (Frakes et al., 1987) it appears that no strong climatic changes affected the continent during that time although minor regional climate variation probably existed (Dettmann et al., 1992). Although rifting continued along Australia's western, southern, and southeastern margins and eastern Australia may have been broadly uplifted (Veevers et al., 1991), the continent did not experience significant mountain-building events in the mid-Cretaceous. The probable absence of a significant geographical or climatic cause for the disappearance of various (mostly deciduous) gymnosperm and herbaceous equisetalean groups might suggest that their demise was a direct response to competition from the emerging angiosperms. While this is difficult to confirm,

especially in the absence of a complete Late Cretaceous floral record, it is pertinent to note that several of these declining plant groups persisted later in the presumably more isolated New Zealand flora (McQueen, 1956; Daniel et al., 1990).

ACKNOWLEDGEMENTS

Alex Cook kindly organised the loan of specimens from the Queensland Museum. Andrew Rozefelds thanks the owners of Cork, Dalkieth, and Whyrallah Stations and other properties in the Winton-Longreach district for their hospitality to Queensland Museum officers during fieldwork in that area. This research was supported by Australian Research Council Grant A19031108 to AND.

LITERATURE CITED

- ANDERSON, J.M. & ANDERSON, H.M. 1985. 'Palaeoflora of southern Africa. Prodrum of South African megaflores Devonian to Lower Cretaceous'. (A.A. Balkema: Rotterdam).
1989. 'Palaeoflora of southern Africa. Moltenu Formation (Triassic) Volume 2. Gymnosperms (excluding *Dicroidium*)'. (A.A. Balkema: Rotterdam).
- ARBER, E.A.N. 1917. The earlier Mesozoic floras of New Zealand. New Zealand Geological Survey Palaeontological Bulletin 6: 1-80.
- ARCHANGELSKY, S. 1965. Fossil Ginkgoales from the Ticó Flora, Santa Cruz Province, Argentina. Bulletin of the British Museum Natural History (Geology) 10: 121-137.
1966. New Gymnosperms from the Ticó Flora, Santa Cruz, Argentina. Bulletin of the British Museum Natural History (Geology) 13: 259-295.
- ARRONDO, O.G. & PETRIELLA, B. 1980. Alicurá, nueva localidad plantífera Liásico de la provincia de Neuquén, Argentina. Ameghiniana 7: 200-215.
- BAKSI, S.K. 1968. Fossil plants from Raghavapuram Mudstone, West Godavari district, A.P., India. Palaeobotanist 16: 206-215.
- BALDONI, A.M. 1979. Nuevos elementos paleoflorísticos de la taflofa de la Formación Spring Hill, límite Jurásico-Cretácico subsuelo de Argentina y Chile austral. Ameghiniana 16: 103-119.
- BOSE, M.N. 1955. Some Tertiary plant remains from Queensland, Australia. Botaniska Notiser 108: 381-390.
1975. *Araucaria haastii* Ettingshausen from Shag Point, New Zealand. Palaeobotanist 22: 76-80.
- BOSE, M.N. & SAH, S.C.D. 1968. Some pteridophytic remains from the Rajmahal Hills, Bihar. Palaeobotanist 16: 12-28.
- BRENNER, G.J. 1984. Late Hauterivian angiosperm pollen from the Helez Formation, Israel, 6th International Palynological Conference, Calgary 1984, Abstracts, p. 15.
- BURGER, D. 1970. Early Cretaceous angiosperm pollen grains from Queensland. Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin 116: 1-15.
1973. Spore zonation and sedimentary history of the Neocomian, Great Artesian Basin, Queensland. Geological Society of Australia Special Publication 4: 87-118.
1980. Palynology of the Lower Cretaceous in the Surat Basin. Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin 189: 1-106.
1988. Early Cretaceous environments in the Eromanga Basin: palynological evidence from GSQ Wyandra-1 corehole. Association of Australasian Palaeontologists Memoir 5: 173-186.
1990. Early Cretaceous angiosperms from Queensland, Australia. Review of Palaeobotany and Palynology 65: 153-163.
1993. Early and middle Cretaceous angiosperm pollen grains from Australia. Review of Palaeobotany and Palynology 78: 183-234.
- CANTRILL, D.J. 1992. Araucarian foliage from the Lower Cretaceous of southern Victoria, Australia. International Journal of Plant Science 153: 622-645.
- CANTRILL, D.J. & WEBB, J.A. 1987. A reappraisal of *Phyllopteroides* Medwell (Osmundaceae) and its stratigraphic significance in the Lower Cretaceous of eastern Australia. Alcheringa 11: 59-85.
- COUPER, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geological Survey Palaeontological Bulletin 22: 1-77.
1960. New Zealand Mesozoic and Cainozoic plant microfossils. New Zealand Geological Survey Palaeontological Bulletin 32: 1-87.
- COWLEY, W.M. & FREEMAN, P.J. 1993. 'Geological Map of South Australia'. (Geological Survey of South Australia, South Australian Department of Mines and Energy, Adelaide).
- CRANE, P.R. & LIDGARD, S. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science 246: 675-678.
1990. Angiosperm radiation and patterns of Cretaceous palynological diversity. Pp. 377-407. In Taylor, P.D. & Larwood, G.P. (eds) 'Major Evolutionary Radiations', Systematics Association Special Volume 42. (Clarendon, Oxford).
- CRANE, P.R., PEDERSEN, K.R., FRIIS, E.M. & DRINNAN, A.N. 1993. Early Cretaceous (Early to Middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac Group of eastern North America. Systematic Botany 18: 328-344.
- DANIEL, I.A., LOVIS, J.D. & REAY, M.B. 1990. A brief introductory report on the mid-Cretaceous megaflores of the Clarence Valley, New Zealand,

- Proceedings of the 3rd International Organization of Palaeobotany Conference, Melbourne 1988: 27-29.
- DAY, R.W., 1964. Stratigraphy of the Roma-Wallumbilla area. Geological Survey of Queensland Publication 318: 1-23.
- DAY, R.W., WHITAKER, W.G., MURRAY, C.G., WILSON, I.H. & GRIMES, K.G. 1983. Queensland Geology. Geological Survey of Queensland Publication 383: 1-194.
- DEL FUEYO, G.M. 1991. Una nueva Araucariaceae Cretácica de Patagonia, Argentina. *Ameghiniana* 28: 149-161.
- DETMANN, M.E. 1973. Angiospermous pollen from Albion to Turonian sediments of eastern Australia. Special Publication of the Geological Society of Australia 4: 3-34.
1986. Early Cretaceous palynoflora of subsurface strata correlative with the Koonwarra Fossil Bed, Victoria. *Memoir of the Association of Australasian Palaeontologists* 3: 79-110.
1989. Antarctica: Cretaceous cradle of austral temperate rainforests? Pp. 89-105. In Crame, J.A. (ed.) 'Origins and Evolution of the Antarctic Biota'. Geological Society Special Publication 47: 89-105. (Geological Society: London).
- DETMANN, M.E. & PLAYFORD, G. 1969. Palynology of the Australian Cretaceous: Pp. 174-210. A review. In Campbell, K.S.W. (ed.) 'Stratigraphy and Palaeontology. Essays in honour of Dorothy Hill', 174-210. (Australian National University Press: Canberra).
- DETMANN, M.E. & THOMSON, M.R.A. 1987. Cretaceous palynomorphs from the James Ross Island area - a pilot study. *British Antarctic Survey Bulletin* 77: 13-59.
- DETMANN, M.E., MOLNAR, R.E., DOUGLAS, J.G., BURGER, D., FIELDING, C., CLIFFORD, H.T., FRANCIS, J., JELL, P., RICH, T., WADE, M., RICH, P.V., PLEDGE, N., KEMP, A. & ROZEFELDS, A. 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research* 13: 207-262.
- DOUGLAS, J.G. 1965. The Mesozoic leaf *Ginkgoites australis* (McCoy) Florin, and *Ginkgoites waarrensis* n. sp. *Mining and Geological Journal* 6: 20-26.
1969. The Mesozoic floras of Victoria, parts 1 and 2. Geological Survey of Victoria Memoir 28: 1-310.
1970. *Ginkgoites multiloba*. A new *Ginkgo*-like leaf. *Mining and Geological Journal* 6: 28-32.
- DOYLE, J.A. & HICKEY, L.J. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139-206. In Beck, C.B. (ed.) 'Origin and early evolution of angiosperms'. (Columbia University Press: New York).
- DRINNAN, A.N. & CHAMBERS, T.C. 1986. Flora of the Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), south Gippsland, Victoria. *Association of Australasian Palaeontologists Memoir* 3: 1-77.
- DRINNAN, A.N. & CRANE, P.R. 1989. Cretaceous palaeobotany and its bearing on the biogeography of austral angiosperms. Pp. 192-219. In Taylor, T.N. & Taylor, E.L. (eds) 'Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana'. (Springer-Verlag: New York).
- ETHERIDGE, R. Jr 1893. The occurrence of the genus *Phyllopteris* (Brong.) Saporta in the Mesozoic beds of Central Australia. Contributions to the Palaeontology of South Australia, 3: 3-6. In, Parliamentary Papers of South Australia, 23.
- FIELDING, C.R. 1992. A review of Cretaceous coal-bearing sequences in Australia. *Geological Society of America Special Paper* 267: 303-324.
- FRAKES, L.A., BURGER, D., APHORPE, M., WISEMAN, J., DETMANN, M., ALLEY, N., FLINT, R., GRAVESTOCK, D., LUDBROOK, N., BACKHOUSE, J., SKWARKO, S., SCHEIBNEROVA, V., MCMINN, A., MOORE, P.S., BOLTON, B.R., DOUGLAS, J.G., CHRIST, R., WADE, M., MOLNAR, R.E., MCGOWRAN, B., BALME, B.E. & DAY, R.A. 1987. Australian Cretaceous shorelines, stage by stage. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59: 31-48.
- GOULD, R.E. 1974. The fossil flora of the Walloon Coal Measures: a survey. *Proceedings of the Royal Society of Queensland* 85: 33-41.
- GUPTA, K.M. 1955. Notes on some Jurassic plants from the Rajmahal hills, Bihar, India. *Palaeobotanist* 3: 1-25.
- HALLE, T.G. 1913. The Mesozoic flora of Graham Land. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-expedition 1901-1903* 3: 1-123.
- HELBY, R., MORGAN, R. & PARTRIDGE, A.D. 1987. A palynological zonation of the Australian Mesozoic. *Association of Australasian Palaeontologists Memoir* 4: 1-94.
- HERBST, R. 1962. Sobre las especies de *Gleichenites* de los sedimentos Baqueroenses de Santa Cruz, Patagonia. *Ameghiniana* 2: 141-147.
- HICKEY, L.J. & DOYLE, J.A. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review* 43: 3-104.
- HILL, D., PLAYFORD, G. & WOODS, J.T. 1966. 'Jurassic fossils of Queensland'. (Queensland Palaeontographical Society, Brisbane).
- HILL, R.S., JORDAN, G.J. & CARPENTER, R.J. 1993. Taxodiaceous macrofossils from Tertiary and Quaternary sediments in Tasmania, Australia. *Systematic Botany* 6: 237-249.
- HUGHES, N.F. & MCDUGALL, A.B. 1987. Records of angiosperm pollen entry into the English Early Cretaceous succession. *Review of Palaeobotany and Palynology* 50: 255-272.

- LIDGARD, S. & CRANE, P.R. 1988. Quantitative analysis of the early angiosperm radiation. *Nature* 331: 344-346.
1990. Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* 16: 77-93.
- LONGOBUCCO, M.I., AZCUY, C.L. & AGUIRRE URRETA, B. 1985. Plantas de la Formación Kachaike, Cretácico de la Provincia de Santa Cruz. *Ameghiniana* 21: 305-315.
- M'CLOUGHLIN, S. IN PRESS. A guide to the Cretaceous plant fossils of Western Australia. Publication of the Department of Earth and Planetary Sciences, Western Australian Museum.
- M'CLOUGHLIN, S. & DRINNAN, A. N. 1995. (This volume). A Middle Jurassic flora from the Walloon Coal Measures, Mutdapilly, Queensland. *Memoirs of the Queensland Museum* 38: 257-272.
- MCQUEEN, D.R. 1956. Leaves of middle and Upper Cretaceous pteridophytes and cycads from New Zealand. *Transactions of the Royal Society of New Zealand* 83: 673-685.
- MAHESHWARI, H.K. & SINGH, N.P. 1976. On some plant fossils from the Pariwar Formation, Jaisalmer Basin, Rajasthan. *Palaeobotanist* 23: 116-123.
- MEDWELL, L.M. 1954a. A review and revision of the flora of the Victorian Lower Jurassic. *Proceedings of the Royal Society of Victoria* 65: 63-111.
- 1954b. Fossil plants from Killara, near Casterton. *Proceedings of the Royal Society of Victoria* 66: 17-23.
- MEHTA, K.R. & SUD, J.D. 1953. On some ginkgoalean leaf impressions from the Rajmahal Hills. *Palaeobotanist* 2: 51-54.
- MOORE, P.S. & PITT, G.M. 1984. Cretaceous of the Eromanga Basin; Implications for hydrocarbon exploration. *Australian Petroleum Exploration Association Journal* 24: 358-376.
- MORGAN, R. 1980. Palynostratigraphy of the Australian Early and middle Cretaceous. *Geological Survey of New South Wales Palaeontological Memoir* 18: 1-153.
- PARRIS, K.M., DRINNAN, A.N. & CANTRILL, D.J. 1995. *Palissya* cones from the Mesozoic of Australia and New Zealand. *Alcheringa* 19: 87-111.
- PETERS, M.D. 1985. A taxonomic analysis of a mid-Cretaceous megaplant assemblage from Queensland. University of Adelaide PhD thesis. 200 pp. (unpublished).
- PETERS, M.D. & CHRISTOPHEL, D.C. 1978. *Austrosequoia wintonensis*, a new taxodiaceous cone from Queensland, Australia. *Canadian Journal of Botany* 56: 3119-3128.
- PLAYFORD, G., HAIG, D.W. & DETTMANN, M.E. 1975. A mid-Cretaceous microfossil assemblage from the Great Artesian Basin, northwestern Queensland. *Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen* 149: 333-362.
- POLE, M. 1992. Cretaceous macrofloras of eastern Otago, New Zealand: angiosperms. *Australian Journal of Botany* 40: 169-206.
- RAINE, J.I. 1984. Outline of a palynological zonation of Cretaceous to Paleogene terrestrial sediments in West Coast region South Island, New Zealand. *Report of the New Zealand Geological Survey* 109: 1-81.
- ROZEFELDS, A.C. 1986. Type, figured and mentioned fossil plants in the Queensland Museum. *Memoirs of the Queensland Museum* 22: 141-153.
- SAH, S.C.D. 1953. On some species of *Ginkgoites* from the Jurassic of the Rajmahal Hills, Bihar. *Palaeobotanist* 2: 55-58.
1965. Palaeobotanical evidence on the age of the Khatangi Beds (? Dubrajpur), in the Rajmahal Hills, Bihar. *Palaeobotanist* 13: 218-221.
- SAH, S.C.D. & JAIN, K.P. 1965. *Ginkgoites rajmahalensis* sp. nov. from the Rajmahal Hills, Bihar, India. *Palaeobotanist* 13: 155-157.
- SENIOR, B.R., MOND, A. & HARRISON, P.L. 1978. Geology of the Eromanga Basin. Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin 167: 1-102.
- SEWARD, A.C. & SAHNI, B. 1920. Indian Gondwana plants: a revision. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, N.S., 7(1): 1-55.
- SUKH-DEV, 1970. Some ferns from the Lower Cretaceous of Madhya Pradesh - 1. *Palaeobotanist* 18: 197-207.
1987. Floristic zones in the Mesozoic formations and their relative age. *Palaeobotanist* 36: 161-167.
- STOVER, L.E. & EVANS, P.R. 1973. Upper Cretaceous-Eocene spore-pollen zonation, offshore Gippsland Basin, Australia. *Special Publication of the Geological Society of Australia* 4: 55-72.
- TAYLOR, D.W. & HICKEY, L.J. 1990. An Aptian plant with attached leaves and flowers: implications for angiosperm origin. *Science* 247: 702-704.
- TOWNROW, J.A. 1967. On *Rissikia* and *Mataia* podocarpaceous conifers from the lower Mesozoic of southern lands. *Papers and Proceedings of the Royal Society of Tasmania* 101: 103-136.
- UPCHURCH, G.R., CRANE, P.R. & DRINNAN, A.N. 1994. The megaflores from the Quantico locality (upper Albian), Lower Cretaceous Potomac Group of Virginia. *Virginia Museum of Natural History Memoir* 4: 1-57.
- VEEVERS, J.J., POWELL, C.McA. & ROOTS, S.R. 1991. Review of seafloor spreading around Australia. 1. Synthesis of the patterns of spreading. *Australian Journal of Earth Sciences* 38: 373-389.
- WALKOM, A.B. 1917. Mesozoic floras of Queensland. Part 1.-continued. The flora of the Ipswich and Walloon Series. (c) Filicales, etc. *Publications of the Geological Survey of Queensland* 257: 1-65.

1918. Mesozoic floras of Queensland. Part 2. The flora of the Maryborough (Marine) Series. Geological Survey of Queensland Publication 262: 1-21.
- 1919a. Mesozoic floras of Queensland, Parts 3 and 4. The floras of the Burrum and Styx River Series. Geological Survey of Queensland Publication 263: 1-77.
- 1919b. On a collection of Jurassic plants from Bexhill, near Lismore, N.S.W. Proceedings of the Linnean Society of New South Wales 44: 180-190.
1921. Mesozoic floras of New South Wales. Part 1-Fossil plants from Cockabutta Mountain and Talbragar. Memoirs of the Geological Survey of New South Wales, Palaeontology 12: 1-21.
- 1928 Fossil plants from Plutoville, Cape York Peninsula. Proceedings of the Linnean Society of New South Wales 53: 145-150.
1944. Fossil plants from Gingin, W.A. Journal of the Royal Society of Western Australia 28: 201-207.
- WHITE, M.E. 1961a. Plant fossils from the Canning Basin, Western Australia. Appendix 6; In Veevers, J.J. & Wells, A.T. The Geology of the Canning Basin, Western Australia. Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin 60: 291-320.
- 1961b. Report on 1960 collections of Mesozoic plant fossils from the Northern Territory. Australian Bureau of Mineral Resources, Geology and Geophysics, Record 1961/146: 1-26. (unpublished).
1966. Report on 1965 plant fossil collections. Australian Bureau of Mineral Resources, Geology and Geophysics, Record 1966/111: 1-10. (unpublished).
1974. Plant fossils from the Gilbert River and Winton Formations, and the Pascoe River area, Queensland. Australian Bureau of Mineral Resources, Geology and Geophysics, Record 1974/159: 1-5. (unpublished).
- WHITEHOUSE, R.W. 1955. The geology of the Queensland portion of the Great Artesian Basin. In Department of the Co-ordinator General of Public Works: Artesian Water Supplies in Queensland. Queensland Parliamentary Papers A, 56-1955. Appendix G: 1-20.
- ZEBA-BANO. 1980. Some pteridophytes from the Jabalpur Formation. Palaeobotanist 26: 237-247.
- ZEBA-BANO, MAHESHWARI, H.K. & BOSE, M.N. 1979. Some plant remains from Pathargama, Rajmahal Hills, Bihar. Palaeobotanist 26: 144-156.

CONTENTS

| | |
|--|-----|
| BERGQUIST, P.R. Dictyoceratida, Dendroceratida and Verongida from the New Caledonia Lagoon (Porifera:Demospongiae)..... | 1 |
| COOK, A.G. Sedimentology and depositional environments of the Middle Devonian lower Fanning River Group (Big Bend Arkose and Burdekin Formation), Burdekin Subprovince, north Queensland | 53 |
| DAVIES, V.T. A tiny cribellate spider, <i>Jamara</i> gen. nov. (Araneae:Amaurobioidea: Midgeeinae) from northern Queensland | 93 |
| FOX, R.C., CAMPBELL, K.S.W., BARWICK, R.E. & LONG, J.A. A new osteolepiform fish from the lower Carboniferous Raymond Formation, Drummond Basin, Queensland. | 97 |
| GARTH, J.S. & DAVIE, P.J.F. A new species of <i>Parthenope</i> (Crustacea: Decapoda: Parthenopidae) from deep-water off northern Queensland | 223 |
| HEATWOLE, H., DE BAVAY, J., WEBBER, P. & WEBB, G. Faunal survey of New England. IV. The frogs..... | 229 |
| MCKAY, R.J. & RANDALL, J.E. Two new species of <i>Pomadourys</i> (Pisces: Haemulidae) from Oman, with a redescription of <i>P. punctulatus</i> (Rüppell) | 251 |
| MCLOUGHLIN, S. & DRINNAN, A. N. A Middle Jurassic flora from the Walloon Coal Measures, Mutdapilly, Queensland, Australia | 257 |
| MCLOUGHLIN, S., DRINNAN, A. N. & ROZEFELDS, A. C. A Cenomanian Flora from the Winton Formation, Eromanga Basin, Queensland, Australia | 273 |
| NOTE | |
| WILKINSON, J. Fossil record of a varanid from the Darling Downs, southeastern Queensland | 92 |